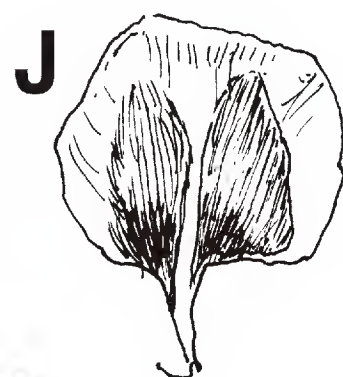
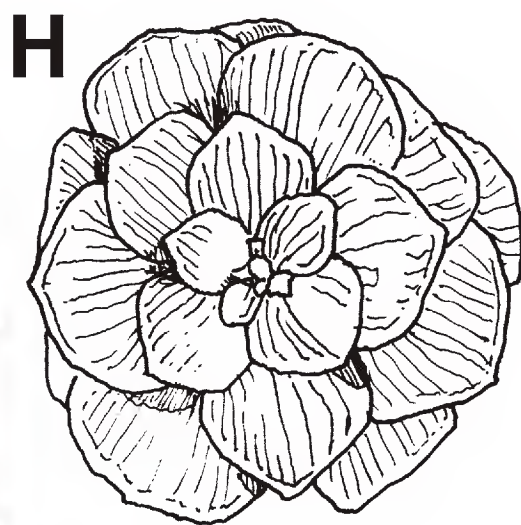
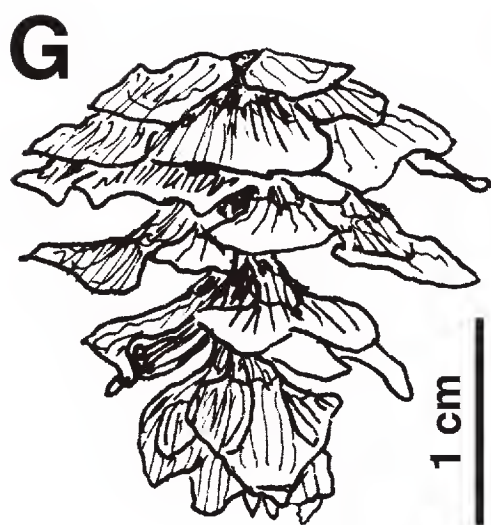
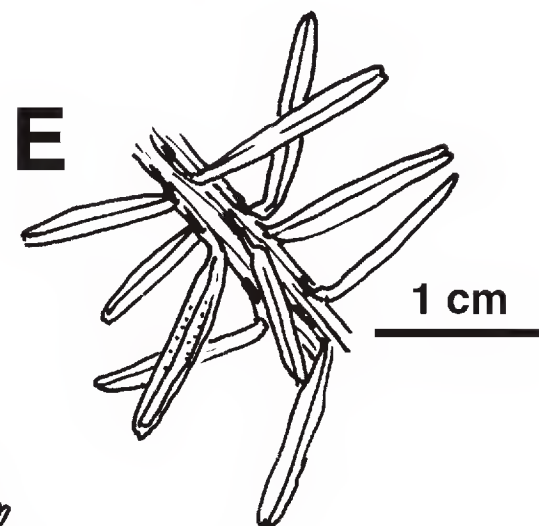
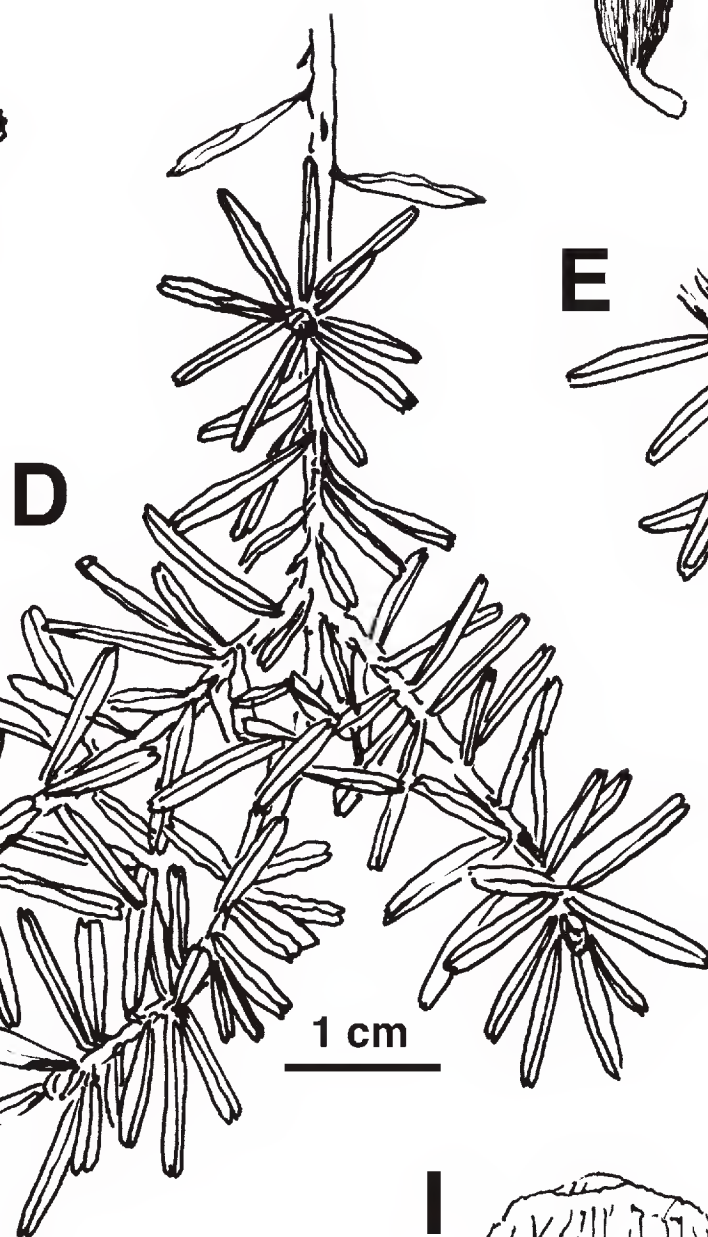
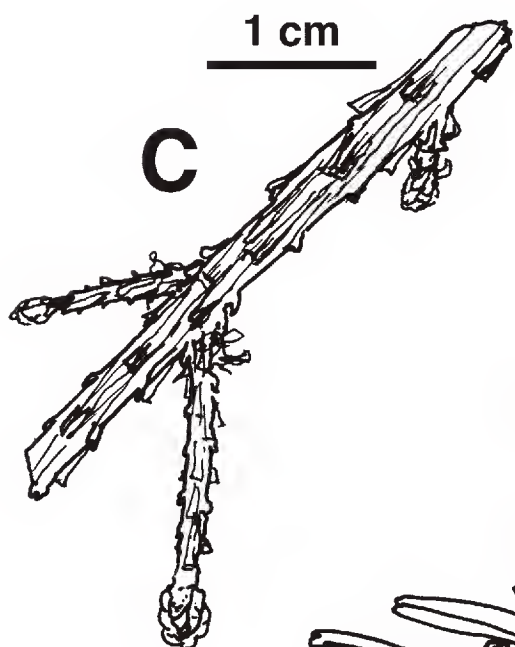
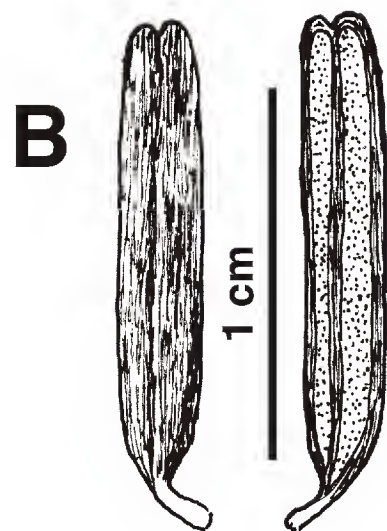
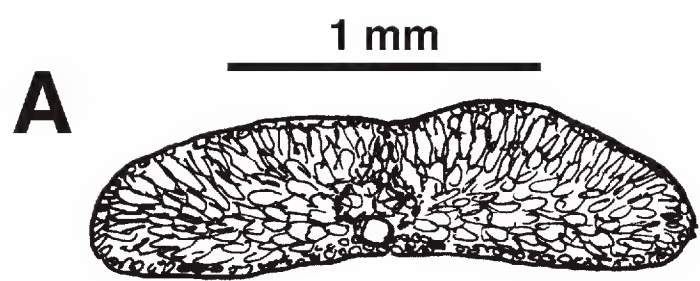


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Front and back cover: Ernest Henry Wilson photographed the dramatic coastline of Ulleungdo, Korea, in 1917, when the island was under Japanese control. In a subsequent 1918 publication, he described ecological “topsyturvydom” on the island, given that “many Alpine plants grow at sea-level and plants which in Japan are found only near the coast grow high up on the mountain-side.” Peter Del Tredici recently worked with collaborators to identify a new species of hemlock (*Tsuga ulleungensis*), which is native to the island. Photo from Arnold Arboretum Archives.

Inside front cover: A version of this illustration accompanied the official description of the Ulleungdo hemlock (*Tsuga ulleungensis*) in *Systematic Botany* in 2017. Illustration by Alison Dibble.

Inside back cover: Although fruits of the hardy kiwi (*Actinidia arguta*, accession 125-40* A) turned a muted red this fall, the interior flesh remained the classic near-fluorescent hue associated with the commercial kiwifruit (*A. deliciosa*). Photo by Jonathan Damery.

Behind the Scenes on Naming a New Hemlock Species

Peter Del Tredici

In my thirty-five years working at the Arnold Arboretum, I have only once been involved in naming a new species—a hemlock tree (*Tsuga ulleungensis*) native to the volcanic island of Ulleungdo in the Sea of Japan. This South Korean island lies 80 miles east of the mainland and 176 miles from the west coast of Japan. It's a small island—twenty-eight square miles—and rises to an elevation of thirty-two hundred feet. Geological records indicate that Ulleungdo emerged from the ocean floor some 2.7 million years ago and that it has been vegetated for the past 1.7 million years. The story of how I got involved with naming this new hemlock tree is complicated, but it bears telling for what it reveals about the process of doing basic botanical research and about how well-documented collections of plants—leavened with a bit of serendipity—can contribute to research on evolution and biogeography.

Although I was not aware of it at the time, my involvement with the plant actually began with the arrival of hemlock woolly adelgid (*Adelges tsugae*) at the Arboretum in 1997. This invasive sucking insect is native to Japan and was discovered in the eastern United States in the 1950s. It took about forty years for the bug to spread from the site of its original introduction in Richmond, Virginia, to the Arboretum—its relentless northward spread driven by warmer winters induced by climate change. When it finally arrived in 1997, it struck with a vengeance, attacking over a thousand trees located on the twenty-two acres of Hemlock Hill and scattered throughout the rest of the grounds. While the insect certainly presented serious problems for the Arboretum, it posed a far bigger threat to the wild-growing hemlocks of southern New England.

In response to the arrival of hemlock woolly adelgid in the Northeast, biologists adopted a multipronged approach to try controlling the pest: Plant physiologists evaluated various chemical controls. Entomologists began

searching for Asian insects that might be used as potential biocontrol. And horticulturists began evaluating other hemlock species for resistance to the bug. Given the Arboretum's extensive collection of hemlock species, which is nationally accredited through the American Public Gardens Association's Plant Collections Network, a number of researchers began coming here in hopes of finding something—anything—that might shed light on the problem and contribute to a solution. Among these researchers was a young graduate student in entomology at Yale University, Nathan Havill, who was also working at the United States Forest Service's Northern Research Station in Hamden, Connecticut, trying to unravel the insect's complex life cycle and assess its genetic diversity across the region.

As luck would have it, Michael Donoghue, a graduate and former professor at Harvard, was on Nathan's dissertation committee at Yale and suggested that just studying the insect was not enough and that Nathan should also do genetic work on hemlock trees. Now anyone who has been a graduate student knows how annoying it can be when a committee member adds more work to a thesis project, but Nathan recognized a good idea when he saw one and agreed to investigate the genetics of the Arboretum's hemlocks in order to create a phylogenetic tree describing their relatedness. For help, he recruited Chris Campbell, a professor at the University of Maine and another Harvard alum, to help with the project because one of Chris's former students, Tom Vining, had produced DNA sequence data on *Tsuga* and developed a rough phylogeny of the genus in 1999.

I first met Nathan in the spring of 2003, when he came to collect hemlock samples at the Arboretum. He was also looking for adelgid galls on the bug's alternate host, the Japanese tiger-tail spruce (*Picea torano*). It wasn't until the following year, having completed his genetic analysis, that Nathan shared the preliminary

results of his research with me and casually mentioned that one of our accessions—labelled as southern Japanese hemlock (*Tsuga sieboldii*), from Ulleungdo, South Korea—did not line up with the Arboretum's other specimens under the same name, which was weird. Our two plants from Ulleungdo (accession 1251-83*A and B) had arrived in 1983 as wild-collected seed obtained by the Chollipo Arboretum, an institution located outside of Seoul, and no one prior to Nathan had questioned their identity.

Despite its small size, Ulleungdo is famous in botanical circles for harboring over thirty species found nowhere else in the world. Ernest Henry Wilson visited the island in the late spring of 1917, guided by the botanist Takenoshin Nakai who was describing the island's plants on behalf of the Japanese government, which had taken over the kingdom of Korea in 1910. Wilson collected herbarium specimens of the hemlocks that he found there and, following Nakai's lead, referred to them as

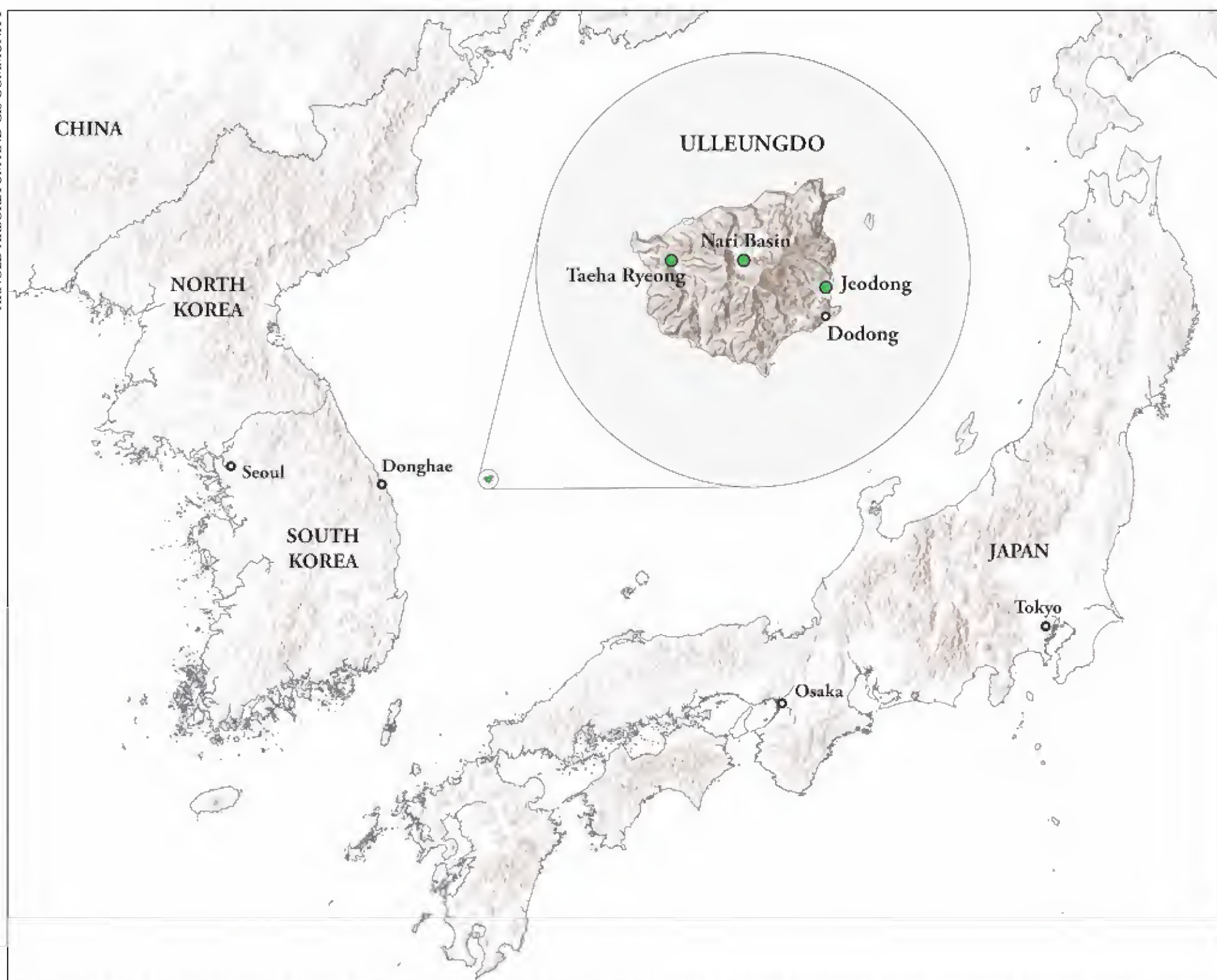
Tsuga sieboldii. This was a logical decision on his part given close morphological similarities with the southern Japanese hemlock and the fact that there were no hemlocks on the Korean peninsula or adjacent parts of China. Nakai's classification held up until 2008 when Nathan published his finding that the Ulleungdo hemlock was genetically distinct from the southern Japanese hemlock. Although Nathan indicated that more detailed analysis was required, his results suggested the taxon was more closely allied with the northern Japanese hemlock (*T. diversifolia*).

A few months before this paper was published, I met up with Nathan at the Fourth Symposium on the Hemlock Woolly Adelgid, held in Hartford, Connecticut, in February 2008. I asked him about the Ulleungdo hemlock, and he told me that his research was inconclusive as to whether or not it was a new species. I was surprised to hear this and immediately asked him if he would have a problem



JONATHAN DAMERY

Two anomalous hemlocks on Bussey Hill became the catalyst for naming a new hemlock species (*Tsuga ulleungensis*), which is endemic to Ulleungdo, South Korea. Accession 1251-83*B is shown here, overlooking the oak collection.



Ulleungdo is a small volcanic island, ecologically isolated within the Sea of Japan. Botanists have discovered more than thirty endemic plant species or subspecies on the island. Collecting locations by Peter Del Tredici and his colleagues are marked.

with me continuing his work on the taxonomic status of Ulleungdo hemlock. That would be fine, he said, because he was now working full time for the Forest Service on the genetics of the hemlock woolly adelgid and had no time for continued research on the trees. He also suggested that I collaborate with Ashley Lamb, an entomologist at Virginia Tech, who was going to southern Japan in the spring to study a potential hemlock woolly adelgid biocontrol insect, a small beetle known as *Laracobius osakensis*. I located Ashley at the conference later that day, and in no time flat, we agreed to collaborate on an Arboretum-funded trip to Ulleungdo. We would collect hemlock leaf samples and look for adelgids that Nathan could sequence for his research.

Not even three months later, on May 9, Ashley and I met in Osaka, Japan, and immediately caught a flight to Seoul. There, we made contact with Nam Sook Lee, a professor at Ehwa Womans University, and her colleague Sung Hee Yeau. I had met Nam Sook several years earlier when she was visiting herbaria in the eastern United States—including Harvard—and we had kept in touch. When I began developing my plans to go to Ulleungdo, Nam Sook generously agreed to host the expedition, which meant making all of the travel arrangements and procuring the permits needed to collect research samples on the island. The four of us left early the next morning on the three-hour drive from Seoul to Donghae, the point of departure for the

ferry to Ulleungdo. It was a clear day, but the seas were rough. Despite my scopolamine patch, I suffered mightily from sea sickness during the seemingly endless journey, as did most of the other passengers on the ship. As far as I could tell, only Ashley, sleeping with her head down on a table the whole time, emerged unscathed.

Needless to say, I was relieved when our ship finally landed at Jeodong, one of the island's two main cities, where we were met by Suk Su Lee, who worked for the local forestry department.

(Later, from 2011 to 2015, he served as chief of forestry for Ulleung County, which also includes forty-three smaller islands). Suk Su quickly found a taxi and took us to our hotel, where I promptly passed out for two hours. He met us later for lunch (which I skipped, still feeling queasy), and then he drove us up into the hills north of Jeodong, nearly one thousand feet in elevation, where I got my first look at the native forest with *Camellia japonica* in bloom in the understory, along with the Ulleungdo beech (*Fagus crenata* var. *multinervis*), which many taxonomists treat as a separate species (*F. multinervis*). We also observed two varieties of maple endemic to Ulleungdo (*Acer mono* ssp. *okamotoanum* and *A. pseudosieboldianum* ssp. *takesimense*), the Japanese white pine (*Pinus parviflora*), and most importantly, the Ulleungdo hemlock, the target of our expedition.

On the second hemlock tree we examined, Ashley found evidence of the adelgid and immediately collected samples for Nathan. We stayed in the area for a couple of hours, collecting more samples of the adelgid as well as herbarium specimens and leaf samples of the hemlocks. On the way down, the sun was setting, and we stopped at the elementary school in Jeodong, where Suk Su proudly showed us three hem-



Dodong, the primary port city for Ulleungdo, is located south of Jeodong. In the foreground, *Sorbus ulleungensis*, an endemic mountain ash, can be seen flowering.

lock trees that he had collected from the forest and planted at the entrance. They were growing extremely well—about twenty-five feet tall and very full—and all three were loaded with developing cones.

We were up early the next day and took a taxi across the island to Taeha Ryeong, a special reserve established in 1962 to protect some of the largest hemlocks, beeches, and Japanese white pines on the island. The slopes were steep, and the hemlocks were especially large in trunk diameter—up to 25.5 inches (65 centimeters). I managed to collect leaf samples from about twenty trees that had branches low enough to reach; all were growing around fifteen hundred feet in elevation. From there, we hiked down the mountain through a patch of woods that harbored an unbelievably rich herbaceous understory. We ended up at a clearing where our taxi driver was supposed to meet us, but since he wasn't there, we took the opportunity to do more collecting. Suk Su, at some risk to life and limb, climbed a tall hemlock and managed to collect a branch with both male and female cones on it, which we had been unable to obtain at our earlier location because the trees were too tall. He climbed down from the tree with the precious specimen just as our cab showed up.



Collaborator Suk Su Lee collected *Tsuga ulleungensis* from the wild and planted three specimens near the elementary school in Jeodong. After Peter Del Tredici visited in the spring of 2008, Suk Su sent seed from these plants to the Arboretum, where they were propagated and planted in the landscape.

From Taeha Ryeong, we drove halfway around the island to the Nari Basin, a volcanic caldera left after an eruption that occurred about ten thousand years ago. This is now the only place on the island with relatively flat ground, so the locals have taken advantage of this fact by establishing agricultural fields devoted to the cultivation of local medicinal plants, such as *Codonopsis lanceolata*, a vining member of the bellflower family (Campanulaceae). The landscape was beautiful, ringed by mountains, with specimens of the Ulleungdo hemlock in the surrounding forest and *Sorbus ulleungensis*, an endemic mountain ash, growing at the edges of the fields. (Incidentally, the mountain ash was then considered to be *S. commixta*—a species that ranges through northern Japan and the islands of eastern Russia—illustrating another case where speciation on Ulleungdo was long unrecognized.) We had lunch at a vegetarian restaurant that served the traditional *bibimbap* dish filled with medicinal plants

cultivated in the caldera and wild plants from the surrounding mountains—super healthy we were told—which was unlike anything I’ve tasted before or since.

The caldera was a jumping-off point for hiking to the highest peak on the island, but it was too late in the day for us to make the trek, so we headed back down the mountain to our hotel. We were greeted with bad news that a storm was moving in and that we would have to leave the island a day earlier than planned or risk getting stuck and missing two lectures I had scheduled in Seoul. The *coup de grace* was that there were no seats left on the boat leaving at five o’clock the following afternoon, so our only choice was to take a ferry at five the next morning. In the absence of any alternative, I packed up the specimens and set my alarm clock. It was frustrating to have come this far only to have the trip cut short before I could finish exploring the island. The good news was that I had collected leaf samples from



Ernest Henry Wilson photographed a stand of hemlocks—now *Tsuga ulleungensis*—on Ulleungdo in 1917, estimating heights ranging to 75 feet (23 meters). Peter Del Tredici observed similarly impressive specimens at the Taeha Ryeong Reserve in 2008, including this tree, which measured 98 feet (30 meters) tall.



thirty-one plants in five different locations, which was enough for a thorough genetic analysis of the Ulleungdo hemlock population.

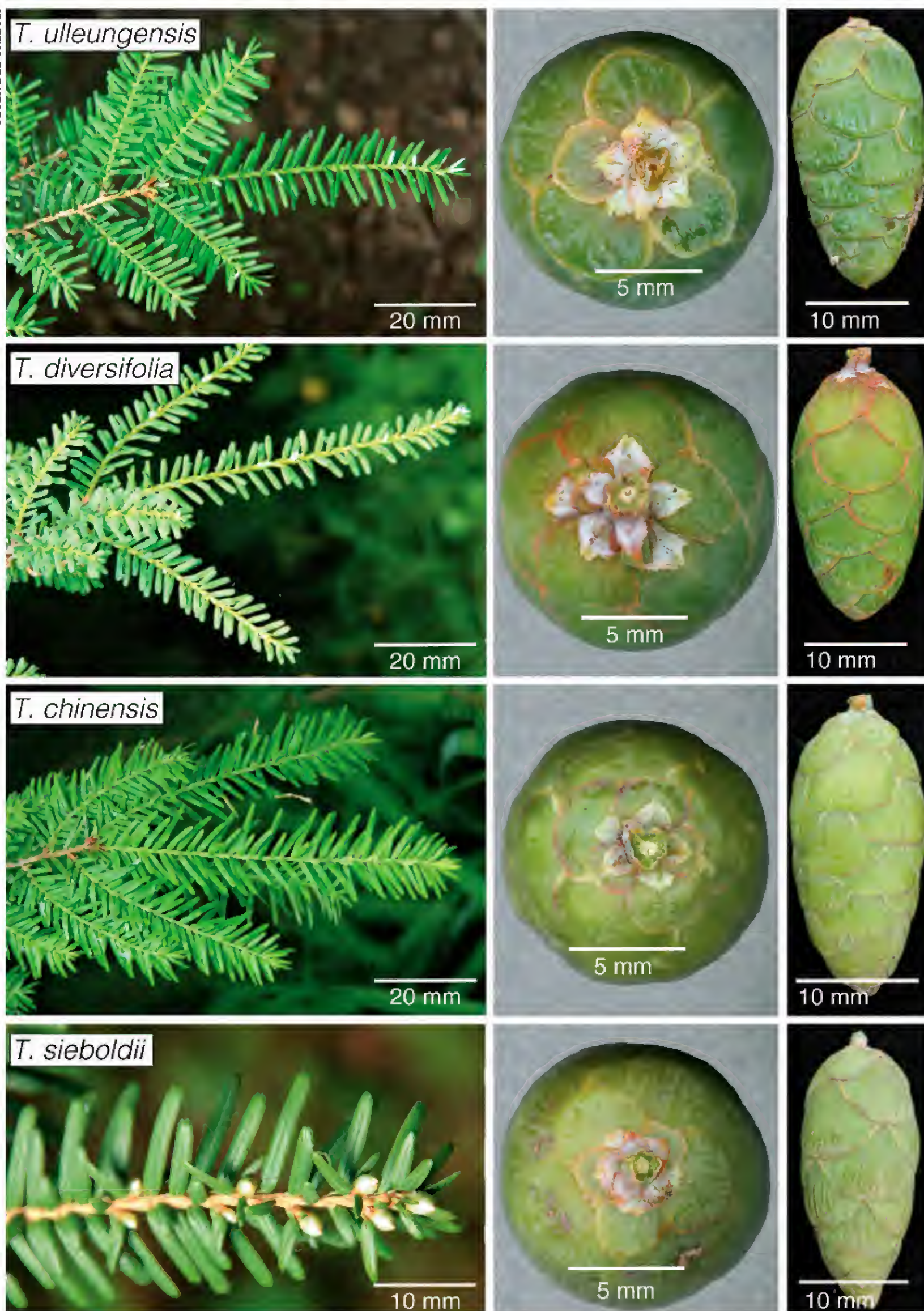
After returning to the Arboretum from Korea, I continued making observations on the leaf and cone morphology of our two specimens of the Ulleungdo hemlock, but I failed to make progress on the genetic analysis of the leaf samples. The breakthrough finally came two years later, in August 2010, at the Botanical Society of America meetings in Providence, Rhode Island. I met with Chris Campbell, the professor from the University of Maine who had collaborated with Nathan on hemlock phylogeny, and his graduate student Garth Holman. After a brief discussion, we all agreed that Garth should include a chapter on the Ulleungdo hemlock in his dissertation on conifer genetics. His research would be based on the Arboretum's trees and on the DNA samples I had collected from Ulleungdo. It was with great joy and relief

that I turned my samples and herbarium specimens over to Garth later that fall—at last they were going to someone who would put them to good use.

For the next four years, Garth labored in the lab on the genetic analysis of various hemlock species, while also assessing their morphological variation. At the same time, I continued with my phenological studies at the Arboretum, which showed that the Ulleungdo hemlock consistently leafed out a few days before *Tsuga diversifolia* and more than a month before *T. sieboldii*. With the help of Arboretum staff member Kevin Block, I also determined that the Ulleungdo hemlock was tolerant but not immune to damage by the hemlock woolly adelgid.

Garth completed his dissertation in September 2014 with a preliminary description of the Ulleungdo hemlock as a new species: *Tsuga ulleungensis*. Going from a dissertation to an actual publication in a scientific journal, however, is not always a quick process. In this case,

PETER DEL TREDICI



Comparison of four Asian hemlocks growing at the Arnold Arboretum. On the left, the branches show simultaneous phenological conditions on May 23, 2012. The central images show the attachment point for the seed cones, where differences in the shape of cone-scale bracts are most evident—providing a subtle but important diagnostic characteristic for the species.

it took Garth another two years to expand and improve the research he had done for his degree, before submitting for publication to *Systematic Botany* in 2017. The final results, which were published in December of that year, painted a complicated picture of the Ulleungdo hemlock's ancestry: its chloroplast DNA indicated a closer relationship to *T. diversifolia* than to *T. sieboldii*, while the nuclear DNA was equivocal about the relationships among the three species. The morphological data—its cone and leaf structure—indicated that the Ulleungdo hemlock was more similar to *T. sieboldii* than *T. diversifolia*. Taken together, this evidence indicates that *T. ulleungensis* is distantly related to both Japanese hemlocks but is probably closer to *T. diversifolia* than to *T. sieboldii*.

The Ulleungdo hemlock is most likely a remnant of a species that was once widespread on the Korean peninsula but disappeared from the mainland as a result of multiple glaciations that took place during the Pleistocene, over the past million or so years. Because of its mild, oceanic climate, Ulleungdo is the only place in Asia where *Tsuga ulleungensis* survived. The existence of some thirty-three other endemic species or subspecies of plants on Ulleungdo provides further evidence that this isolated landmass has long served as a glacial refugium.

To me, the most interesting thing about the *Tsuga ulleungensis* story is how it illuminates the role that well-documented living collections can play in supporting basic scientific research and conservation. We start with a graduate student sampling the collections and finding a genetic anomaly. Next, we check the records to see where the plant originated, and then, in collaboration with scientists from the host country, we go back to the original location to recollect the plant for more in-depth analysis. Without the Arboretum's well-managed curatorial system, it would be impossible to make any of these connections. In the case of the Ulleungdo hemlock, a plant growing inconspicuously on the grounds of the Arboretum for twenty years unexpectedly provided a key to understanding the complex evolutionary history of a species restricted to a tiny

island off the coast of Korea—half a world away. From a research perspective, the Arboretum's collections are a means to an end rather than an end in themselves: they provide easy access to a significant percentage of the world's temperate trees and shrubs and are the perfect jumping-off point for any number of studies that can open the doors to basic evolutionary questions.

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Dormant Vines, Future Wines

Al Kovalski and Jason Londo

When you sip an aromatic Riesling with dinner in September, the day may feel noticeably shorter than it did a month before. While fall officially starts with the autumnal equinox, which occurs between September 21 and 24 from year to year, day length continuously decreases after the summer solstice and will continue through the arrival of winter. From August to November, in fact, the days get shorter by almost three minutes per day in Boston. Plants, including the common grapevine (*Vitis vinifera*), pay close attention to day length from the moment leaves and flowers unfurl in the spring until fruit ripens and leaves drop. Although this internal clock may seem difficult to conceptualize—more esoteric than flavor and mouthfeel, or even pests and diseases—understanding the process by which plants enter and exit dormancy, and how they survive in between, is critical, especially as winegrowers (and other agricultural producers) adapt their production to withstand a changing climate.

As grapevines grow, they form buds in the leaf axils. Within these buds, about ten nodes are pre-formed—leaf primordia (baby leaves) and inflorescence primordia (baby flowers). These buds are formed in preparation for the following growing season. In that way, wines produced in 2018 actually started as microscopic inflorescences in the summer of 2017, which overwintered inside buds, formed flowers that bloomed in the spring of 2018, and became fruit that was harvested in the late summer and fall, effectively spending over a year developing on the plant alone. This process doesn't happen only in *Vitis vinifera*, the species native to the Mediterranean from which most of our wines are produced. Wild grape species like the riverbank grape (*V. riparia*), which is native to North America, and gloryvine grape (*V. coignetiae*), which ranges from eastern Russia to Japan, go through the same process, as do the majority of temperate perennial plants.

Unlike migratory birds that avoid winter by flying south, plants are stationary. Therefore, plants must endure low temperatures and other unsuitable growing conditions that come with the winter. In these conditions, they lower their metabolism and enter dormancy, much like hibernation for animals. Plants, however, have evolved to start the preparation for winter much before damaging temperatures arrive, without relying on year-to-year weather patterns. Leaves register the decreasing day length (or technically the increasing nighttime), which provides a signal for buds to enter dormancy. Plants then start changing color to create the beautiful spectacle of fall foliage. In this process, grapes relocate nutrients from the leaves into storage tissue in the woody vines, ready to be recycled the following year. Once plants lose their leaves, they no longer track the day length. Instead, grapevines know when to start growing in the spring by tracking how long they have been cold.

Much like a person setting an alarm to have eight hours of sleep, buds count the number of hours spent in what are called chilling temperatures, between 32 and 50°F (0 and 10°C). Just as different people need different amounts of sleep to be productive, each grapevine species, and even different genotypes within a single species, have different chill requirements before they are able to come out of dormancy. Once they have accumulated enough chilling hours, buds are able to better respond to warm temperatures and produce spring growth. The chilling requirement is associated with the region where a species originated: species from lower latitudes are accustomed to low chill accumulation because of short winters, while species from higher latitudes have a high chill requirement because of longer winters. Given that no chill accumulation occurs below 32°F (0°C), however, plants growing in cold continental climates, like Minnesota, or much higher latitudes, like northern Canada, expe-



Because species and cultivars of grape (*Vitis*) can be grown in a wide range of temperate climates, they prove valuable for studying how hardy plants endure cold weather. At left, October snow clings to *Vitis vinifera* 'Cabernet Sauvignon' in Geneva, New York. Other species, like riverbank grape (*V. riparia*), shown at right, are even better adapted to cold temperatures.

rience low chill accumulation. Species from these places, therefore, also tend to have a low chill requirement.

Chill requirements prevent plants from resuming growth during midwinter warm spells, which could cause death of both flowers and leaves upon the return of cold weather. The mechanisms that make buds wait for the appropriate and consistent warm weather in the spring are still largely unknown, but solving this mystery is important. As temperatures continue to increase due to climate change, the amount of chilling that plants experience in different areas is changing: lower latitudes are experiencing fewer hours with chilling temperatures, whereas the opposite is true for higher latitudes, like Boston and upstate New York. This trend in northern areas may seem a little counterintuitive, but time that was previously spent in

below-freezing temperatures is now rising into the chilling range, above freezing but below 50°F (10°C), causing chill accumulation to rise.

When plants fail to accumulate the necessary chilling requirement, they have erratic, reduced, and delayed budbreak. In vineyards and orchards, this means reduced yields. The same is true with native forests, where flowering and corresponding seed production drops. Moreover, shifting phenology could detrimentally impact overlap between flowering and the activity of pollinators for a given species, or there may be competition due to overlapping flowering for species that were previously staggered. In areas where excessive chill is expected, more responsive plants may break buds during midwinter warm spells, when they previously would have known to wait. In agricultural settings, new cultivars and adaptive management practices can



Grapevines, like those in this commercial vineyard in Geneva, New York, gradually prepare for cold temperatures by tracking the increasing length of uninterrupted nighttime in the fall.

help overcome these effects in the short term. For forests, however, climate change is happening faster than floristic composition can change. Researchers at the University of Alberta, in Canada, have estimated that forest species are already 80 miles south of their optimal climate niche, and this figure is expected to increase to 190 miles in the 2020s, beyond recorded rates of natural forest migration.

Dormancy Fundamentals

Vitis is a compelling genus to study dormancy because of its distribution from tropical to subarctic regions. Even the common grapevine (*V. vinifera*) alone is capable of growing within a wide band of climates, with the majority of production in the Northern Hemisphere spanning latitudes between San Diego and Vancouver (30 to 50° north). In the Southern Hemisphere, the band is even wider, stretching from northern Argentina to southern New Zealand (20 to 50° south), with some production occurring as close to the equator as northeastern Brazil (9° south).

Moreover, many of the most popular cultivars like *V. vinifera* 'Pinot Noir' and 'Chardonnay' are present in almost all of these areas, which demonstrates the remarkable plasticity of the species. Also, many varieties have been cultivated for a very long time. The first records for 'Riesling' date from the fifteenth century—before Columbus arrived in the Americas—and impressively, seeds of 'Rkatsiteli' were found in clay vessels dating to 3,000 BC. 'Rkatsiteli' is still grown in Georgia, the eastern European country where the archaeological discoveries occurred, and limited production can be found in the Finger Lakes wine region of New York. This historical continuity provides us with a wealth of records from different regions, providing both temporal and geographic context for understanding the basic requirements for dormancy of grapevines.

Measuring the chilling requirement of different grapevine varieties can be very simple, and in fact, similar techniques can be used to study dormancy in most deciduous perennial plants.

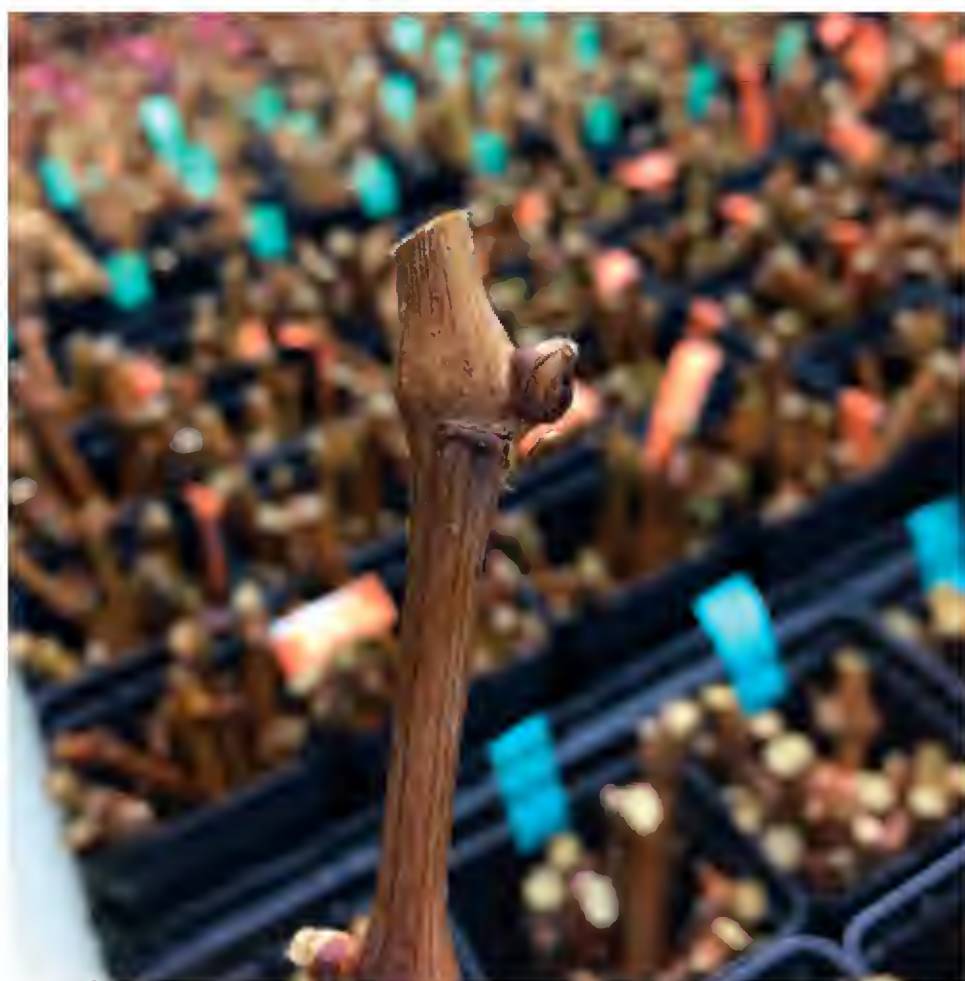


Once leaves have dropped, buds in the vineyard will wait to unfurl until a specified amount of chilling temperatures has been experienced.

Cuttings with dormant buds that have experienced different amounts of chill are placed in a warm environment (72°F or 22°C) with sixteen hours of daylight. The chilled buds can either be collected from the field in regular intervals throughout the winter, or collected in late fall or early winter and placed in a cold chamber where they'll be removed after certain doses of chilling have been provided. The number of days taken for budbreak decreases for buds that have experienced additional chilling. When at least 50 percent of the buds have expanded within twenty-one days of being put into warm conditions, the buds are considered to have fulfilled dormancy requirements, and have now moved into a different phase in the dormancy cycle.

Dormancy can be divided into three phases. *Paradormancy* occurs during the growing season due to factors that arise outside the bud tissue, typically from plant hormone concentrations. For example, hormones produced in the shoot tip prevent lateral growth too close to the tip. This phenomenon, known as apical

dominance, dictates the general conical shape of spruce trees (*Picea*), for instance, because the uppermost buds are more suppressed than the lower buds. Because grapevines are pruned, paradormancy is minimized, allowing lateral branching throughout the growing season. *Endodormancy* occurs when factors within the bud prevent growth. This phenomenon is triggered by decreasing day length and temperatures in the autumn. Endodormant buds resist growth, even when taken from the outside and placed in a warmer environment. *Ecodormancy*, as the prefix *eco* hints, occurs when environmental factors prevent the resumption of growth. Buds transition from endo- to ecodormancy through chill accumulation. Essentially, plants clock how long the winter has been, and this tells them whether they should grow when exposed to warm temperatures (spring has arrived), or if they should remain dormant (midwinter warm spell). Once the buds are ecodormant, they will only remain in a dormant state so long as temperatures remain low.



The authors collect dormant grapevine samples and expose the buds to incremental durations of cold in the laboratory, testing the mechanisms by which plants know to produce new growth (including flower buds, shown above) in the spring.

The necessity for chilling is one of the major factors that determines the distribution of vineyards in subtropical and temperate climates. In regions where insufficient chilling occurs naturally, grapevines and other fruit tree species require extra help to transition from endo- to ecodormancy. Wine growers can apply artificial stressors, such as agrochemicals (e.g. hydrogen cyanide), natural compounds (e.g. garlic extract), or even heat from mobile ovens, to jolt endodormant buds into an unnatural ecodormant state, much like a blaring alarm clock. Yet even though these methods can bypass chilling requirements, none are capable of stimulating budbreak as synchronously as natural processes.

In addition to dormancy, plant tissues must have mechanisms to cope with below-freezing temperatures. Leaves and other green tissues are generally very sensitive to freezing, due in part to their high water content. This is why deciduous plants lose their leaves in the fall. In the case of grapevines, buds survive the winter through a process called supercooling. The precise mechanisms that contribute to differences in supercooling ability are exceptionally complex and not well characterized, but at the most basic level, supercooling allows water

to be cooled below 32°F (0°C) and remain liquid. In fact, given the right conditions, water can remain liquid to temperatures around -40°F (-40°C), although once frozen, the water will only melt at 32°F (0°C). You might have observed this phenomenon if you have ever left a water bottle in your car overnight when the temperature dropped below freezing. When you grab the bottle the following morning, the water may still be liquid, but when you shake the bottle, ice will immediately start forming. Supercooling does not necessitate altering the concentration of sugars or other metabolites—the antifreeze method used in a car engine—rather, with grapevines and many temperate fruit species, physical barriers to ice formation seem to play major roles in the supercooling process.

Supercooling provides variable levels of cold hardiness for grapevine buds throughout the winter. If the outside temperature drops below the current level of cold hardiness, ice will form inside the bud tissues, killing the tiny leaves and flowers beneath the bud scales. This means that the threshold temperature for ice formation changes throughout late fall, winter, and early spring. As temperatures begin to dip below freezing in the late fall, grapevine buds slowly

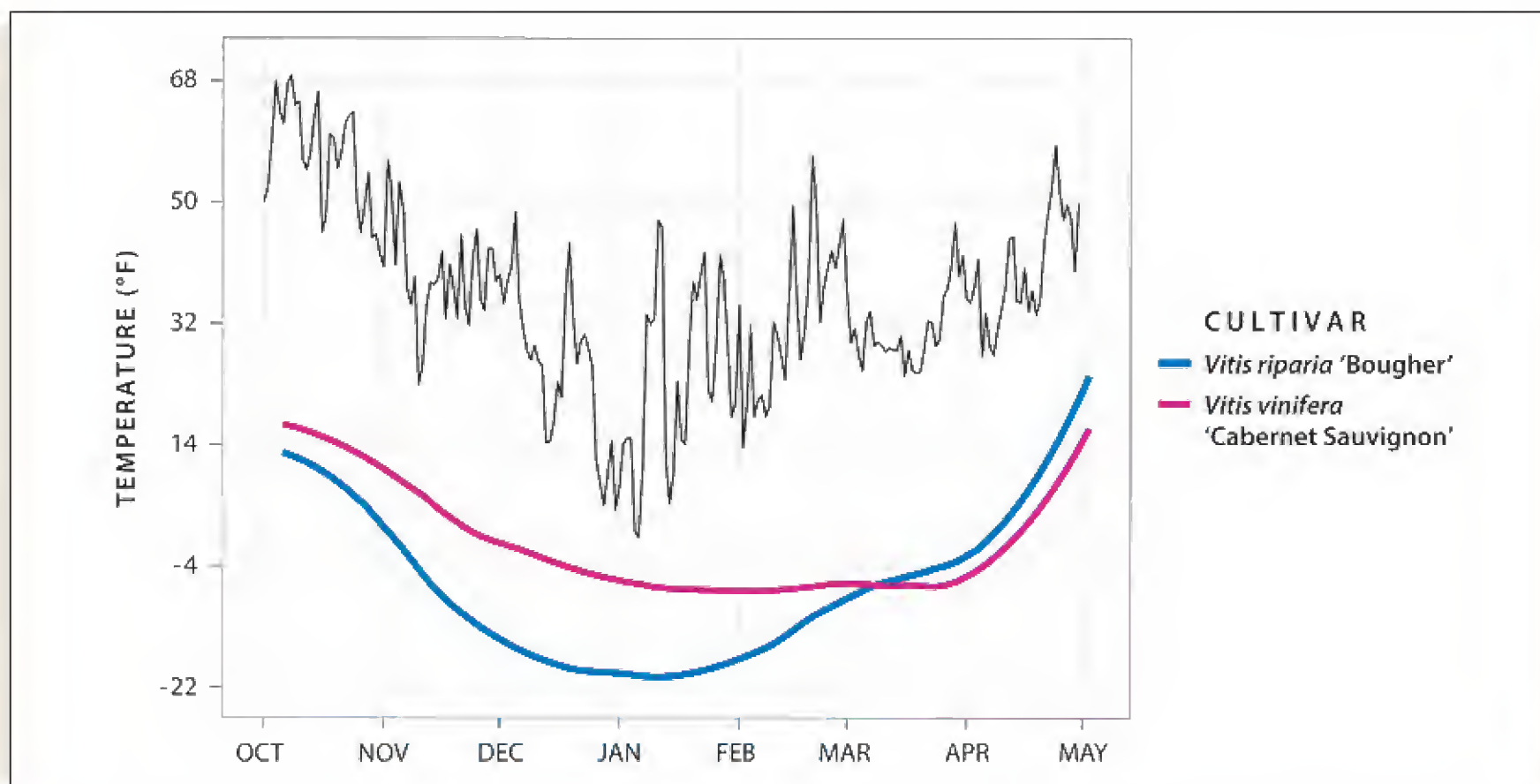
begin to gain cold hardiness, gradually increasing their ability to survive freeze events. The buds always must remain ahead of the environmental temperature, which is very important, and in New York, the first freeze event of the season rarely occurs before grapevines have gone dormant due to this process of acclimation. Under artificial conditions in growth chambers, we have found that if temperatures are held or oscillated around 27°F (-3°C), dormant buds can acclimate to survive temperatures as low as -4°F (-20°C). But the process isn't instantaneous and may take up to two weeks.

Dormancy Danger

Understanding the mechanics of dormancy matters because winter is dangerous for grapevines and other perennial plants, and when it comes to agricultural production, predictable harvests are paramount. Depending on the climate of different grape-growing regions, the most perilous time of winter can differ. In New York, slow temperature decline during the fall helps grapevines fully prepare for winter. In contrast, in the Pacific Northwest—an increasingly respected wine region, known for producing European-inspired vintages—the coldest

days of the year are often in early December, and rapid temperature changes can zap buds before the acclimation process is finished.

Wine growers in New York don't escape unscathed; instead problems arise due to mid-winter cold temperatures. Because the vast majority of commercial grape cultivars have been selected from *Vitis vinifera*, the only grapevine species native to the Mediterranean and therefore adapted for hot summers and mild winters, these cultivars can only survive to a maximum cold temperature of around -4 to -13°F (-20 to -25°C). This temperature range is not unheard of in upstate New York, often causing at least partial bud dieback each winter—the reason vineyards in this region are mostly located around the Finger Lakes and on the shores of the Great Lakes. About sixty wild grape species can be found across North America and Asia, and most have greater maximum cold hardiness than the common grapevine. For example, the fox grape (*V. labrusca*)—the North American species from which 'Concord' grapes were selected—can endure temperatures around -22 to -31°F (-30 to -35°C), or even lower. Amur grape (*V. amurensis*), which has a broad distribution throughout eastern Asia, may be capable



The rates of cold acclimation and deacclimation differ from species to species, and even between different genotypes of the same species. Cold hardiness for cultivars of riverbank grape (*Vitis riparia* 'Bougher') and a common grapevine (*V. vinifera* 'Cabernet Sauvignon') are shown relative to temperature fluctuations in Geneva, New York, throughout months spanning 2017 and 2018. Notice how the riverbank grape—adapted for a colder climate in North America—prepares more rapidly for more severe winter temperatures.

of surviving even lower levels. But while these species seem to promise natural cold hardiness for breeding efforts, our ability to tap into this genetic variation is relatively limited, given that pure water can only supercool to about -40°F (-40°C). Thus, winemakers in regions where winter temperatures drop below this level must be satisfied with importing grapes.

If grapevine buds survive acclimation and midwinter temperatures, the next major event occurs when the buds start losing their cold hardiness as spring temperatures warm. We call this process deacclimation. This is another time of great risk, and climate change promises to make this transition even more unpredictable. Climate models suggest that polar vortex events will become more common in late winter and early spring, catching buds during deacclimation and resulting in lethal damage. Luckily, different species deacclimate at different speeds. The riverbank grape (*Vitis riparia*) tends to be much faster than the common grapevine (*V. vinifera*), for instance, while the southern wild grapevine (*V. cinerea*) seems to be much slower. This difference in northern and southern species probably indicates natural adaptations as a result of their respective winter climates. As a northern species, *V. riparia* probably evolved a fast deacclimation rate to take advantage of the shorter summers, while *V. vinifera* and *V. cinerea*, each more adapted to milder winters and hotter summers, lack the adaptive need to race toward growth. In this way, wild grapevines provide us with the natural adaptive differences needed to learn about cold hardiness and dormancy, and also with the breeding material needed to meet the challenges of a changing climate.

Climate change has already reduced the amount of winter chill accumulation in most traditional wine regions. Bordeaux, the largest winegrowing area in France, now receives about 75 percent of the chilling it had in the mid-1970s. Our latest research has demonstrated that the speed of early spring development is dependent on chill accumulation, and that we can measure this speed based on deacclimation. So to understand the implications of current climate trends in regions like Bordeaux, more detail must be added to our analogy of

dormancy as a night of sleep. When you sleep only one to two hours and get up, it feels like you have not rested at all. Once you hit three hours, every additional hour of sleep feels like a great improvement—think about the difference between four and five hours—although after seven hours, each additional hour provides less energy improvement. We were able to measure a similar phenomenon with the grapevine buds. With minimal chill accumulation, the buds lost their hardiness very slowly, but once they accumulated about eight hundred hours, there was a sharp increase in how responsive they were to warm temperatures. After about twelve hundred hours, however, there was little improvement to responsiveness—the equivalent of surpassing seven hours of sleep. In this sense, the transition between endo- and ecodormancy is gradual, not a clear dichotomy between states.

What does this mean for viticulture? Despite the reduced chill accumulation in Bordeaux, mentioned above, the region still receives plenty of chilling for *Vitis vinifera* cultivars. As a result, the buds and vines are usually ready to begin growing as soon as spring temperatures warm. In 2017, however, unseasonal warmth in April caused early budbreak as plants were very responsive due to high chill accumulation. A subsequent frost occurred in late April and caused extensive damage to vines, reducing the crop by 40 percent compared to the previous year, resulting in one of the lowest yields in the past thirty years. Thus, the future for wine production is complicated from the standpoint of dormancy, cold hardiness, and sustainable viticulture. Climate models predict less chill in warm regions in the future, leading to a need for different cultivars or the use agrochemicals to force vines. In cooler regions, increased chilling temperatures between 32 and 50°F (0 and 10°C) may lead to earlier budbreak for current cultivars, which could be especially detrimental given the increasingly erratic patterns of late winter cold events.

Production of wine is not the main concern with a changing climate, given that food production and broader ecosystem stability are at risk. While our research has focused on grapevines, we expect that similar behavior would be seen with many other horticultural and forest



MICHAEL DOSMANN

Gloryvine grape (*Vitis coignetiae*, accession 63-92*A) at the Arnold Arboretum was wild collected outside of Sapporo, Japan, where record winter lows have hit -19.3°F (-28.5°C) and where average winter snowfall tops seventeen feet (nearly six meters).

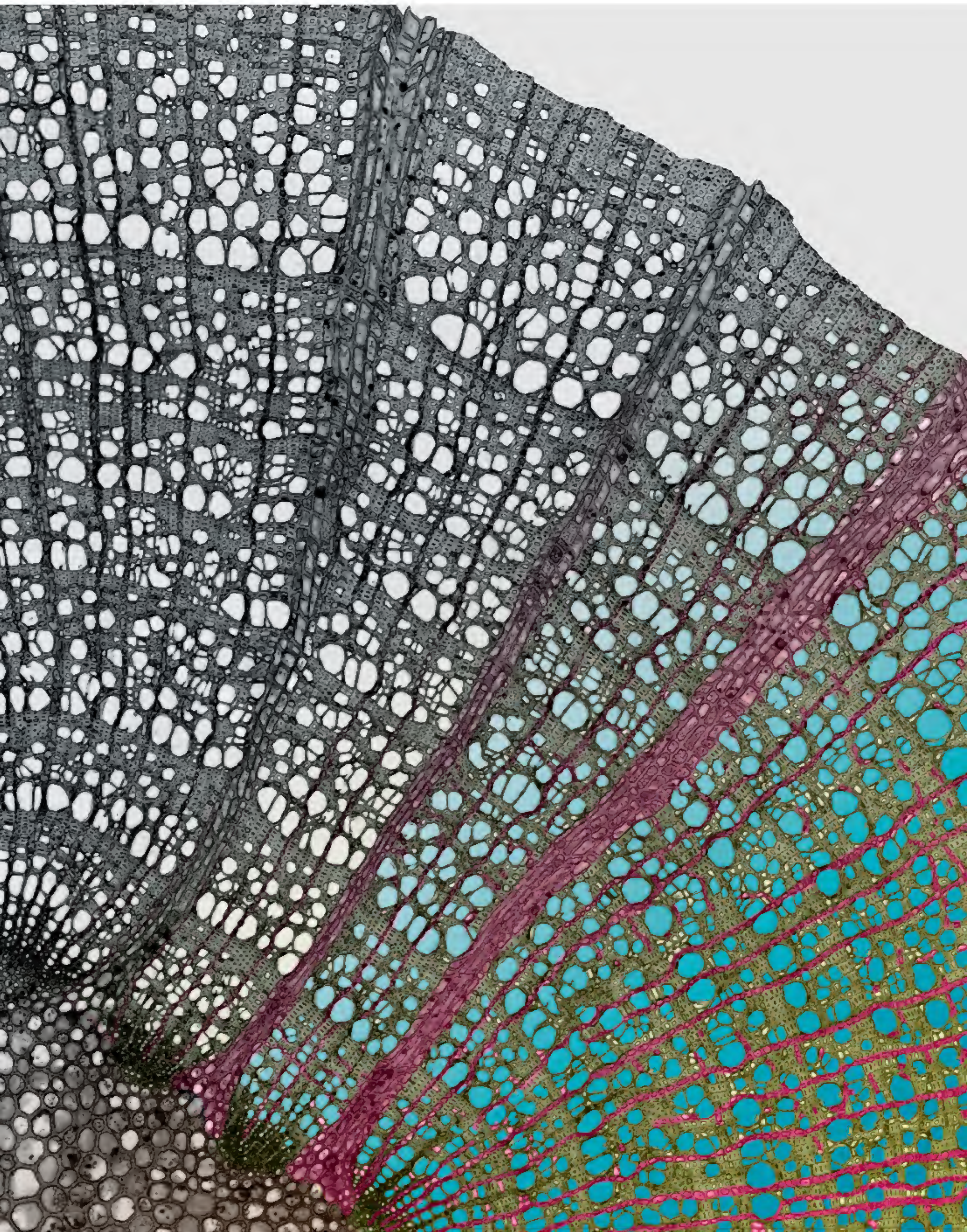
species. Plant distribution is governed by temperature, and these are generally predicted to increase in the future. This means the optimal zones for many plants will move towards the poles—especially if they require chilling. Agricultural production can more readily adapt with new cultivars and species, but forests may need a hand if we want to continue seeing the current diversity available. Minimum temperatures are the most limiting factor for plant distribution, so as the world gets warmer, it is perhaps a little ironic that increasing our understanding of how plants respond to cold may be key to predicting how they will survive in the future.

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WOOD UNDER THE MICROSCOPE

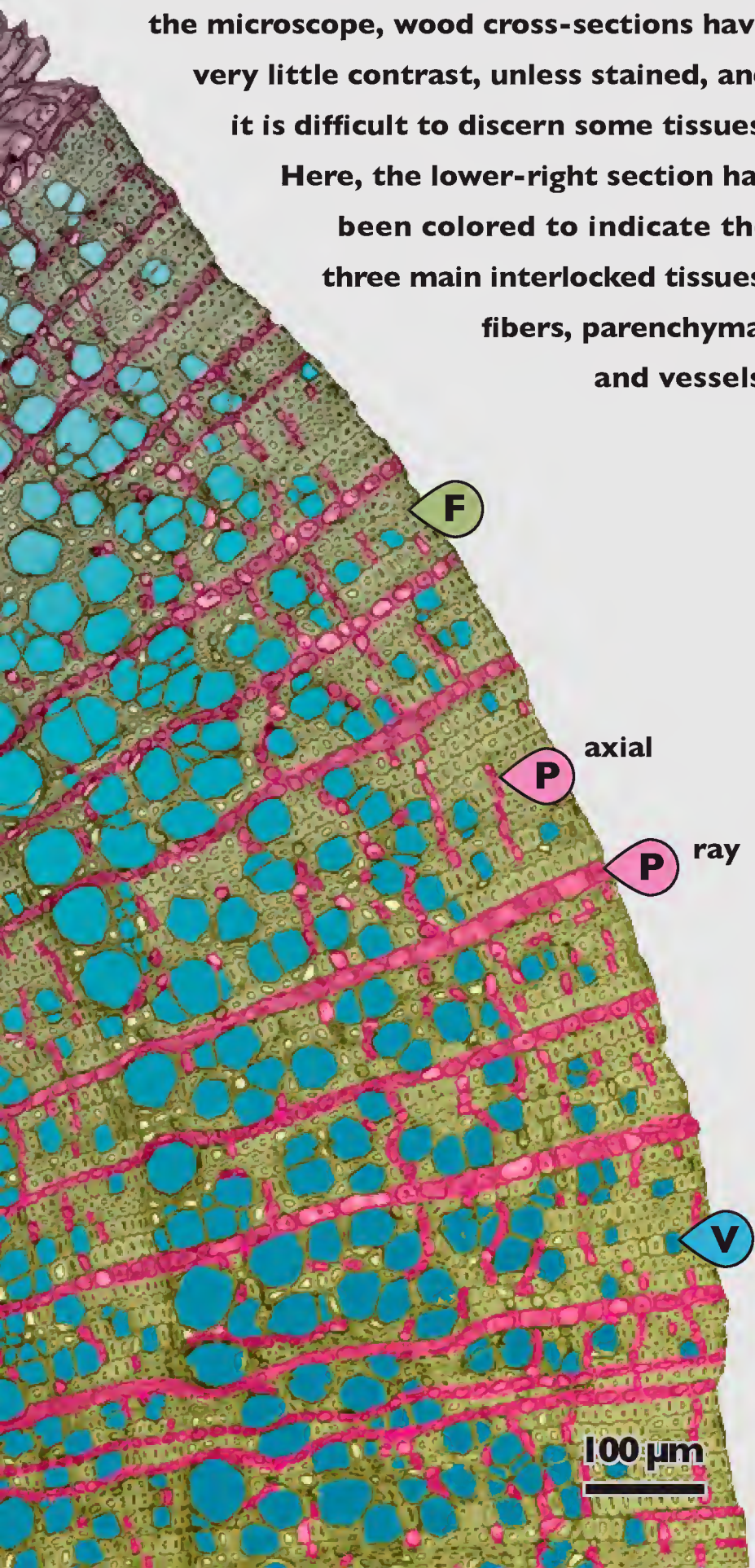
Kasia Ziemińska

The photo below shows the microscopic structure of twig wood from an American beech (*Fagus grandifolia*, accession 683-2008*A) growing at the Arnold Arboretum.

The cross-section is about 10 μm thick, photographed at 200 \times magnification. Under the microscope, wood cross-sections have very little contrast, unless stained, and it is difficult to discern some tissues.

Here, the lower-right section has been colored to indicate the three main interlocked tissues:

fibers, parenchyma, and vessels.



Wood—also called xylem—provides mechanical support for plants, transports and stores nutrients, and transports water from roots to leaves. The proportion, structure, and spatial connectivity of wood tissues varies tremendously across species worldwide, but the functional meaning of much of that diversity remains unclear, leaving much for researchers to discover.

FIBERS look like small donuts within a cross-section. But in fact, they are elongated spindle-like cells. Across species worldwide, fibers are the most abundant wood tissue on average, but their proportion ranges from around 10 to 95 percent. In this American beech, fibers occupied 32 percent of twig wood volume and had medium-thick cell walls. Fibers primarily provide mechanical stability for plants—the strength to support limbs and resistance to environmental stresses like wind or snow.

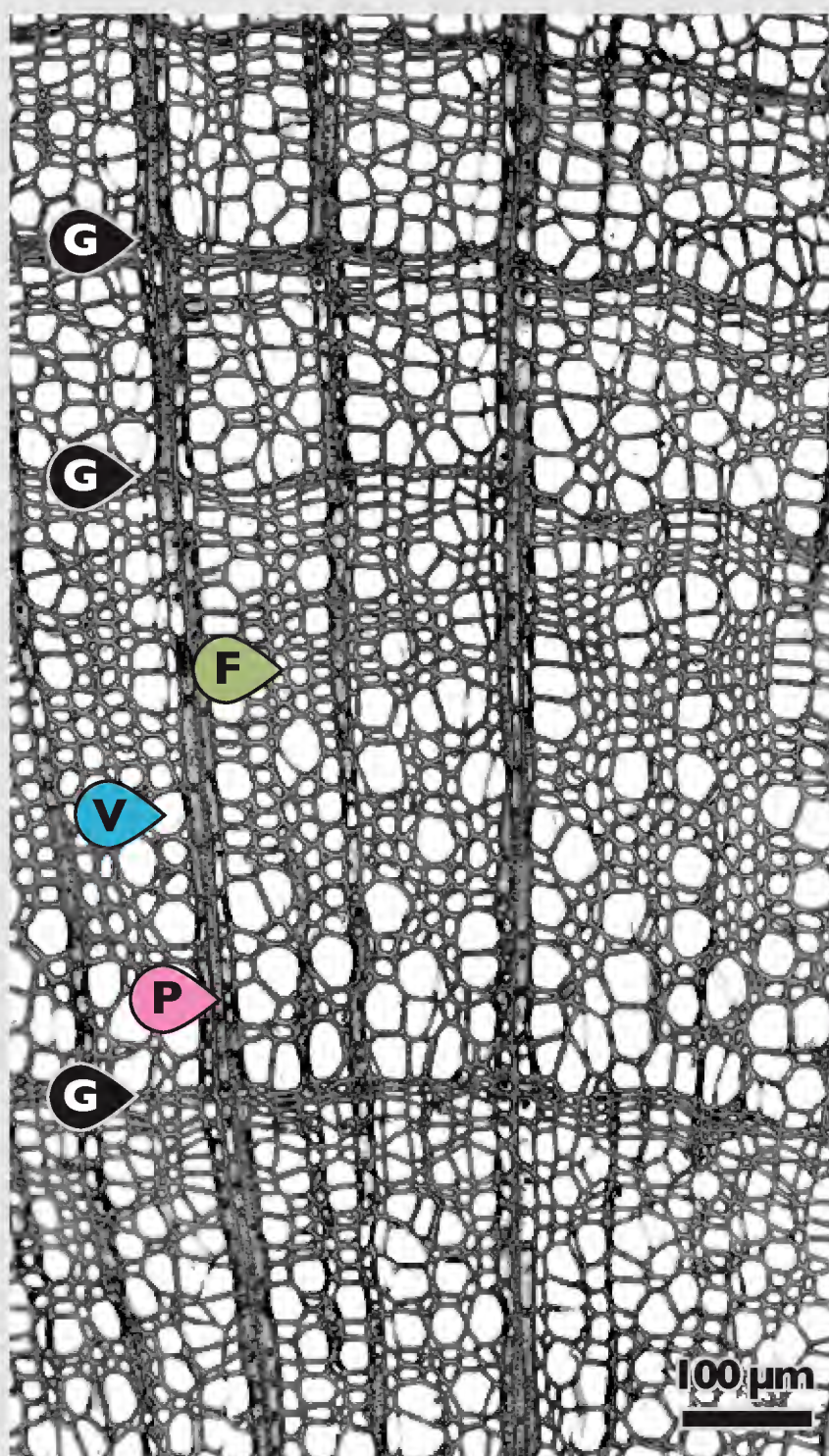
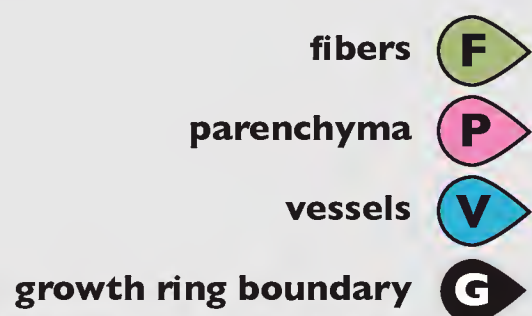
PARENCHYMA is a three-dimensional network of living cells, with *ray parenchyma* connecting bark with inner portions of the stem and *axial parenchyma* running parallel with the length of the stem. This network stores and transports nutrients, which provide energy for building and maintaining living tissues. Parenchyma also contributes to pathogen defense, and it may factor into water storage and the continuity of water transport, although the exact mechanisms of these functions are yet uncertain. Parenchyma occupies between 5 and 90 percent of wood volume for species globally. In this American beech, parenchyma occupied 30 percent.

VESSELS are like pipes that transport water from roots to leaves. Their diameter is larger than other wood cells, and they differ tremendously across species, ranging from around 15 to 250 μm . The diameter has a huge influence on how efficiently water can be transported through wood. The larger the vessel, the more efficient the transport. In this American beech, average vessel diameter was 20 μm .

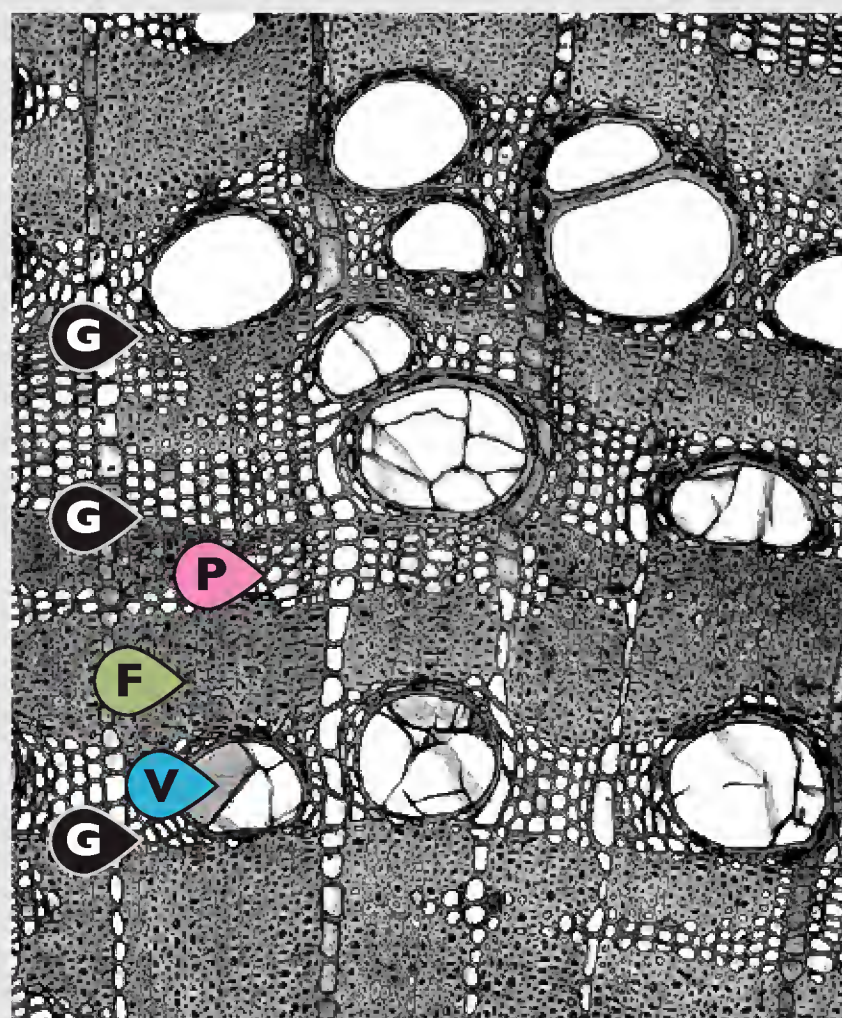
- F** fibers
- P** parenchyma
- V** vessels

Wood samples from seven tree species at the Arnold Arboretum illustrate striking differences in wood anatomy, even among trees adapted for similar climates. Notice the small but relatively consistent diameter of vessels in *Liriodendron*, compared to the prominent seasonal variation in the *Quercus* sample. Likewise, other tissues show similar diversity of dimension and distribution.

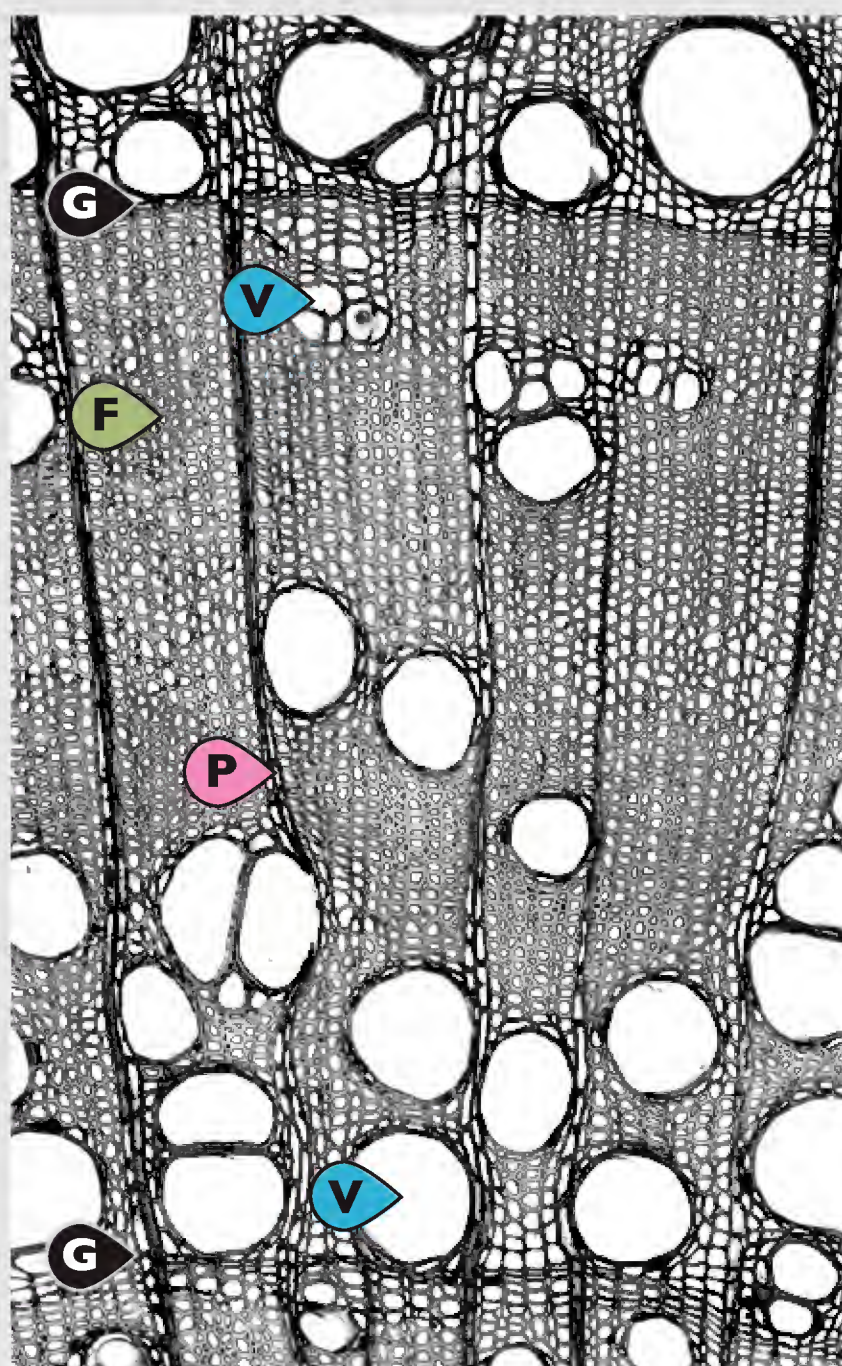
Photos are all at the same scale, so cell sizes can be compared. Each image shows one or more growth rings.



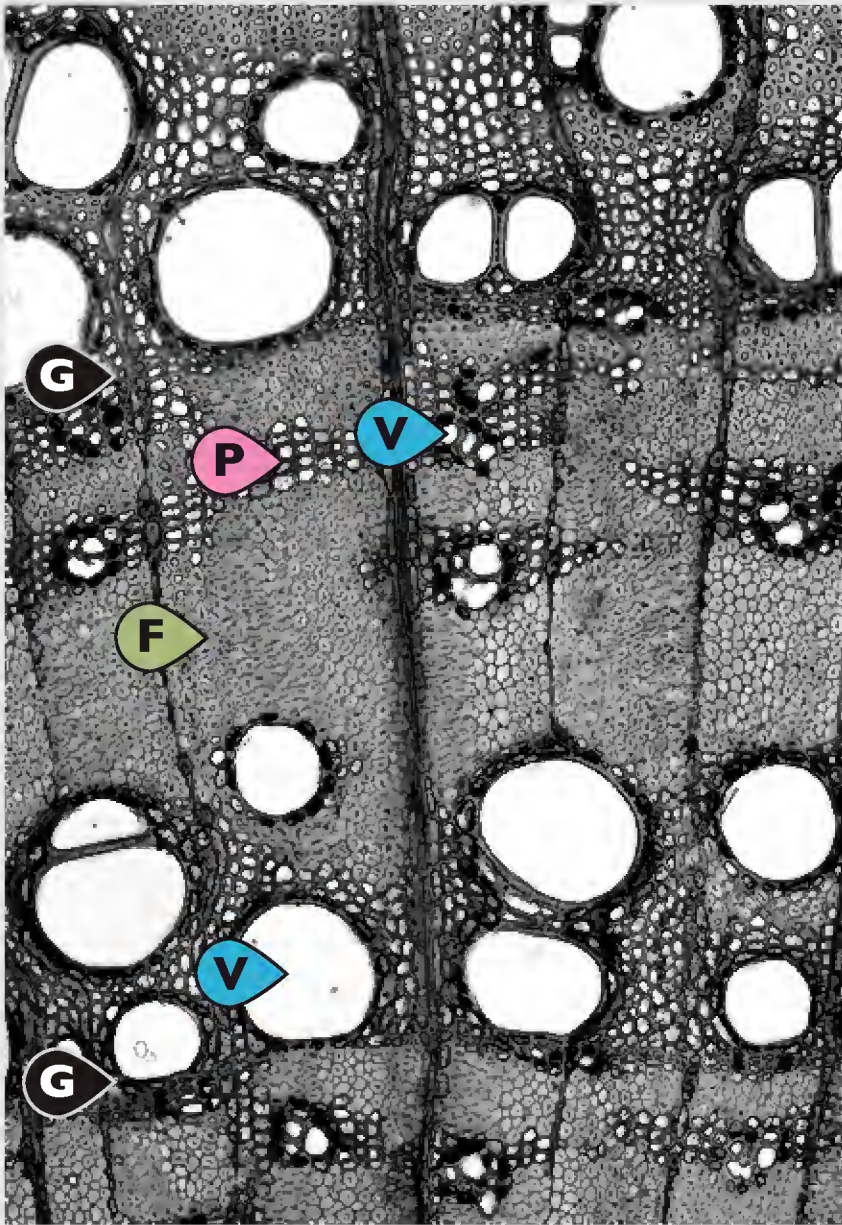
Tulip tree (*Liriodendron tulipifera*, 14992*A)



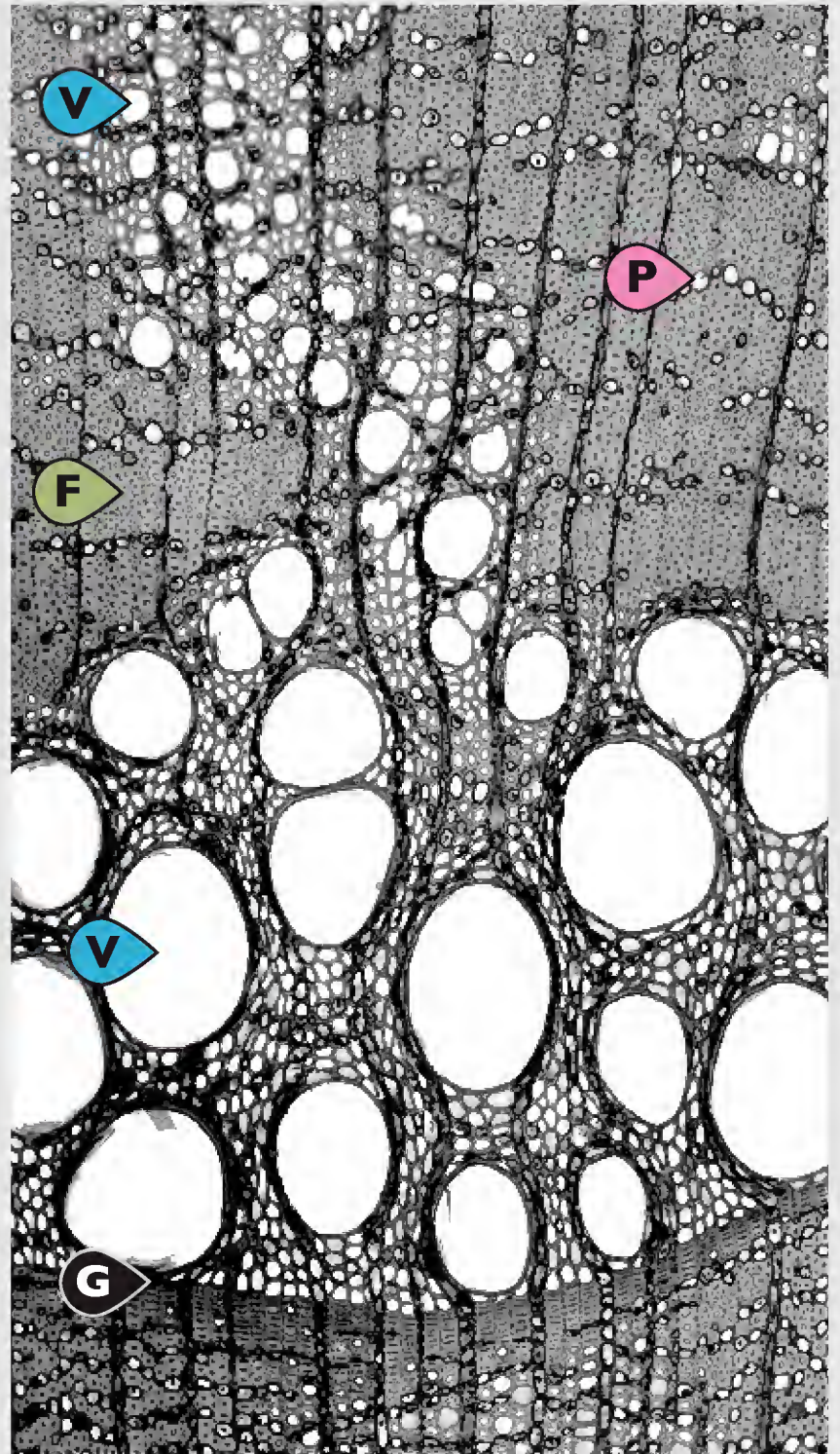
Osage orange (*Maclura pomifera*, 79-46*D)



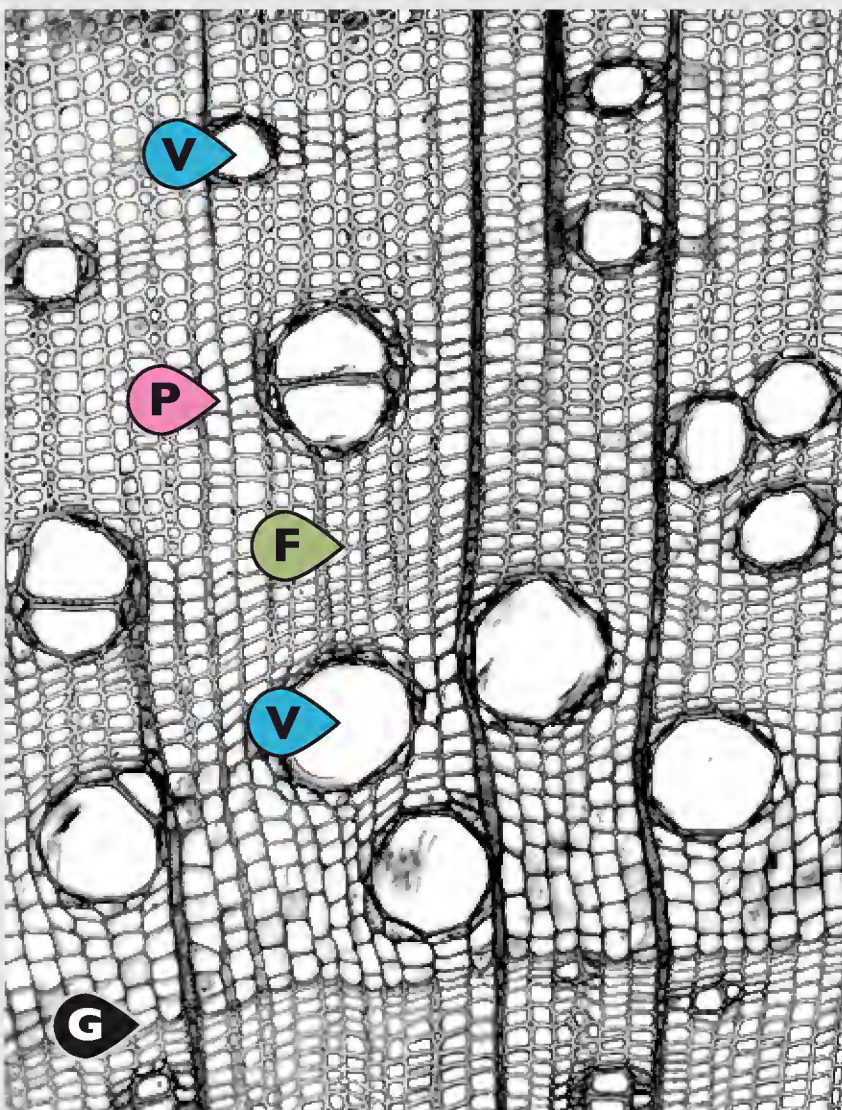
Northern catalpa (*Catalpa speciosa*, 927-58*B)



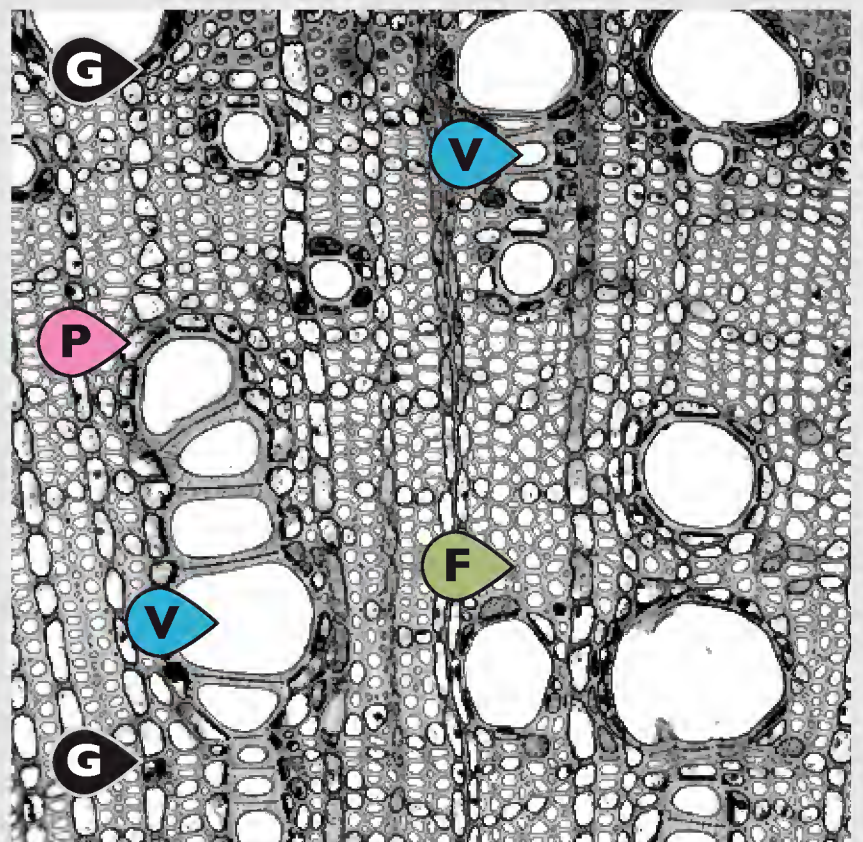
Honeylocust (*Gleditsia triacanthos*, 14681*A)



Chinkapin oak (*Quercus muehlenbergii*, 389-91*C)



Korean paulownia (*Paulownia tomentosa* 'Coreana', 730-77*D)



Common persimmon (*Diospyros virginiana*, 14513*B)

THE ANATOMY OF TREE LIFE

There are myriad ways plants can make a living. Herbaceous annuals grow fast and live short, while other plants, like trees, grow slow and live long. Plants can produce cheaply built leaves that catch sunshine for only a few months, and others produce robust leaves that survive for several years. In a forest, shade-tolerant trees produce short stems, while sun-thirsty ones stretch tall. This marvelous diversity of form and function persists at the microscopic level, hidden to the naked eye yet biologically consequential.

Wood anatomy is not a new discipline. It has been studied since the seventeenth century, when Robert Hooke famously turned a microscope to a sample from the cork oak (*Quercus suber*) and coined the term *cell* based on the walled structures he observed. Shortly thereafter, in 1673, Antonie van Leeuwenhoek began observing the microscopic structure of cross-sectioned twigs from numerous woody species, including temperate and tropical plants. Over the next several decades, he rendered remarkably detailed illustrations, which are among the earliest progenitors to the images shown on the following pages.

Yet the intensity and emphasis of these anatomical studies has changed with time. An increased interest in wood anatomy in the nineteenth century was related to taxonomy—classifying differences between groups of plants—and Harvard University and other institutions built large collections of wood samples (usually rectangular blocks), which allowed researchers to easily compare wood from various species. This descriptive research continued into the twentieth century, although most of the studies were of qualitative nature, where anatomical structures were described using categories like “thin” and “thick,” instead of unit measurements. Over the past sixty years (and especially over the last two decades), however, an increased number of researchers started quantifying anatomical features, and importantly, they began considering the relationship between structure and function of wood on an ecological and climactic scale—attempting to understand why species adapted to disparate habitats possess different wood anatomies.

The three main wood tissues—fibers, parenchyma, and vessels—are also present in herbaceous plants, simply in different organizations. These tissues play several vital functions. They transport water and nutrients, while also providing nutrient storage, pathogen defense, and mechanical support. We are still learning about additional roles; for example, scientists have found that nutrients stored in wood might be used for maintenance of continuous water transport, not only for building new organs like bark and leaves.

Of the three main tissues, researchers have the greatest understanding of vessels, the cells responsible for transporting water. The average size of vessels varies hugely worldwide, from around 15 to 250 μm in diameter. We know that large vessels tend to be more susceptible to embolism—air blockage in a vessel—which impedes water transport and, if common, can be lethal. Embolism can be caused by freeze-thaw events or drought, so species exposed to such stresses tend to have smaller vessels. On the other hand, smaller vessels are less efficient for water transport. Beyond vessel diameter, plants can make many other anatomical adjustments to alter their hydraulic functioning. Some plants have lots of vessels, others very few, and plants can change the size of these structures across the growing season. (On the previous pages, large vessels can often be observed at the beginning of each growing season, when plenty of water was abundant, and the dimensions progressively shrink throughout

the season.) Plants can also change how vessels are interconnected via the shape and size of small openings called pits.

Because anatomical measurements are time consuming, studies that look at highly detailed anatomy are usually limited to, at most, a few dozen species. Recent use of meta-analysis, however, has combined data from many individual studies, shedding light on anatomical variation worldwide—primarily for vessel diameter, vessel proportion, and parenchyma proportion.

As a Putnam Fellow at the Arnold Arboretum, my research focused on parenchyma, the tissue that is understood to store and transport nutrients, along with providing pathogen defense and water storage. One of the large-scale analyses had recently revealed that, across more than fifteen hundred species worldwide, the proportion of parenchyma in wood varies remarkably, ranging from 5 to 90 percent of the total volume (Morris et al., 2016). Species with the highest parenchyma proportions are only found in the tropics, yet species with little parenchyma are found in all climates: temperate, subtropical, and tropical. The functional meaning of this geographical distribution remains unclear, however, which is astonishing considering the dramatic extent of the variation.

Given the traditional understanding that parenchyma stores water, I investigated the hypothesis that woody species with a higher proportion of parenchyma would have greater water-storage capacity, allowing them to withstand drought more readily—essentially like having more water bottles in the pantry. Across thirty tree species that I studied in the Arnold Arboretum, however, species with more parenchyma didn't necessarily store additional water, nor were they better at accessing whatever water had been stored. So the mystery of parenchyma proportion in wood continues to be unresolved. Presumably species with little parenchyma have entirely different life strategies than species with lots of parenchyma. This information will be important for helping us predict how plants will respond to increased aridity in many areas under climate change.

An anatomical perspective within plant sciences is essential for unravelling ecological and physiological questions about how species evolved to grow where they do. William Louis Stern—a professor at the University of Maryland—noted the need for this interdisciplinary approach in the pages of *Arnoldia* back in 1973. “Lest I am accused of being a wood anatomy bigot,” he wrote, “let me hasten to say that I do not believe that studies in wood anatomy can remain viable in a vacuum; rather, they must be integrated with other studies in plant anatomy and with other phases of botanical endeavor.” Wood anatomy is time-consuming and slow—requiring patience and meticulous microscopy skills—but the more we know, the more we realize that we still have much to learn.

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Kasia Ziemińska is an Arnold Arboretum research associate and a recent postdoctoral Putnam Fellow.

Old Molecules, New Climate: *Metasequoia's* Secrets

Hong Yang and Qin Leng

Around forty-five million years ago, the Arctic was ice free, scarcely the expanse of lichen-encrusted rock and glaciers that we see there today. Fossil records reveal that an extensive forest flourished throughout the early Cenozoic, when the canopy was predominated by *Metasequoia* and other deciduous conifers. The single remaining species of this genus, *M. glyptostroboides*, is known as the dawn redwood and is now restricted to a small population in south-central China, around forty-two hundred miles (sixty-eight hundred kilometers) south of this historic distribution. When botanists first learned about the living population more than seventy years ago, no one could have imagined that those plants would provide crucial clues for understanding more than one hundred million years of historic climate change—not to mention changes to come. Yet the rare discovery of fossils containing exquisitely preserved organic tissues and biomolecules, coupled with new molecular research techniques, has revealed just that.

Traditional paleobotanical studies are comparative—drawing links between the anatomy of fossils and their living relatives—while molecular analyses of isotopes and biomolecules (such as lipids, carbohydrates, and lignin) are usually reserved for modern samples of freshly harvested material. Recent innovations with laboratory instruments, however, have made it possible for researchers, including ourselves, to extract valuable molecular information from so-called rocks. With *Metasequoia*, which boasts a long fossil record, the implications of this research are especially pronounced given that we can test hypotheses at the molecular level across an enormous timescale.

The Green Arctic

Scientists (and museumgoers) usually encounter two types of plant fossils: either imprints or compressions. Imprints are analogous to animal tracks, occurring when plant tissue remains pressed into sediments and subse-

quently decomposes, while compressions occur when the tissue becomes sandwiched between flattened layers of sedimentary rocks. In the late 1990s, however, Ben LePage and Chris Williams, then working at the University of Pennsylvania, showed us three-dimensionally preserved *Metasequoia* fossils that they had collected from the Canadian islands of Ellesmere and Axel Heiberg, on the northwestern side of Greenland. We could hardly believe that the fossils were from Cenozoic strata that was around fifty millions years old. The dark-brown leaves, stems, and cones resembled a pile that someone had raked in their backyard—loose but delicate, soft but brittle, individually separated but tightly packed.

When *Metasequoia* lived in the warm and humid Arctic, the plants shed their leaves in autumn, before the four months of total darkness. The litter was buried for tens of millions of years, including beneath the weight of a continental ice cap. Ironically, the tundra surface in the high Arctic has been increasingly exposed due to recent global warming, revealing some of the best fossil material to study ancient climate change. The unrivaled quality of these mummified *Metasequoia* fossils extends beyond what was visible to the naked eye. Using molecular technologies, we detected biomolecules—plentifully! Although cellulose and other polysaccharides are abundant in living plant tissues, they are rarely found in ordinary fossils. Preserved for around fifty million years, these *Metasequoia* fossils possess the oldest biomolecules of this kind ever recovered. Moreover, our molecular evidence suggests that these molecules actually provide both the physical enforcement and chemical stability for maintaining the three-dimensional structures of these exceptional fossils.

The Arctic plays a crucial role in the dynamics of Earth climate. Not only does it actively influence climate on a global scale, but the Arctic passively receives climate change feedback as well. Interestingly, *Metasequoia* has been a witness

CHRISTOPHER J. WILLIAMS



QIN LENG AND HONG YANG



CHRISTOPHER J. WILLIAMS

Fossilized *Metasequoia* trunks from the late Paleocene and early Eocene have been discovered on Ellesmere Island, Canada, along with three-dimensionally preserved leafy fossils, from which the authors have extracted biomolecules and isotope signals. The leafy branchlet in the upper right corner measures 0.83 inches (2.1 centimeters) long.

and faithful recorder of such changes. At Axel Heiberg and Ellesmere Islands, with latitudes higher than 80° north, large amounts of fossilized *Metasequoia* trunks—up to twenty-six feet (eight meters) long and ten feet (three meters) in diameter at breast height—indicate the large size of these forests, which were nurtured by a warm and humid high-latitude climate.

Williams and colleagues demonstrated that the productivity of these dense *Metasequoia* forests was comparable with modern-day temperate rainforests, like the rich landscape of the Olympic Peninsula in Washington State. Yet the *Metasequoia* landscape was primarily populated with deciduous plants, not evergreens—evidence of adaptations for four months of complete darkness at the northern latitudes. Animal fossils are rarely found with these *Metasequoia* remains, but fossils found in similar-aged strata at Ellesmere Island include rhinoceros- and hippo-like mammals, along with giant tortoises and alligators—all indicative of a humid swampy environment, consistent with the reconstruction by plant fossils. Clearly, the ice-free Arctic during the early Cenozoic was a completely different world compared with the barren landscape today.

Living Climate Legacies

To understand the climate that supported such impressive forests in the Arctic, however, our ability to study a living *Metasequoia* species is essential. The first climate-related experiment involving the living species, *M. glyptostrobooides*, was launched inadvertently. When trees were discovered in western Hubei Province, China, in 1944, two American scientists immediately recognized the importance of this plant: Ralph Chaney from the University of California, Berkeley, and Elmer Merrill, the director of the Arnold Arboretum. Through separate collaborations with Chinese colleagues—notably Wan-Chun Cheng and Hsen-Hsu Hu—both Chaney and Merrill arranged for the collection of dawn redwood seeds from China and distributed them to botanical gardens around the United States and Europe. Despite their arguments about who should get the credit for making these seeds available for cultivation, the resulting widespread dispersal to gardens in dra-

matically different climatic zones (essentially all corners of the contiguous United States) set up a natural experiment that we have dubbed the Chaney-Merrill Experiment.

The remnant population of *Metasequoia* in China represents a relatively homogenous genotype, so we can obtain information about how the seedlings survived in disparate gardens, and eliminate some confusion about nature versus nurture. Physiological studies based upon samples from these trees revealed that *M. glyptostrobooides* can endure a wide range of climate conditions. We have obtained leaf samples from forty trees across this range, and these are stored in our Laboratory for Terrestrial Environments at Bryant University, tightly packed in yellow envelopes and frozen. These leaf tissues have helped us generate systematic molecular and biochemical data, which we compared with climate data from the past seventy years from the locations where the trees have been growing. We found that biomolecular compositions within the leaves changed relative to latitude, average temperatures, and average annual precipitation. These correlations established a necessary baseline for interpreting biomolecules and biochemicals that we would later obtain from *Metasequoia* fossils.

Another recent experiment on *Metasequoia glyptostrobooides* provided additional context. Richard Jagels and his colleagues and students at the University of Maine designed a greenhouse experiment to examine how the genus would have performed within its historic distribution inside the Arctic Circle. The climate in this northern region was temperate during the early Cenozoic, yet the unique light regime would have remained consistent: up to four months of complete darkness and four months of twenty-four-hour sunshine. To test the physiological adaptation of *M. glyptostrobooides*—as a living stand-in for the Cenozoic species, *M. occidentalis*—to this light regime, the team partitioned a large greenhouse on their campus into two different compartments: one with normal light, corresponding to the middle latitude of Maine (45° north), and the other with continuous light, mimicking the same low angle and low intensity of Arctic light conditions during summer months.

KYLE PORT

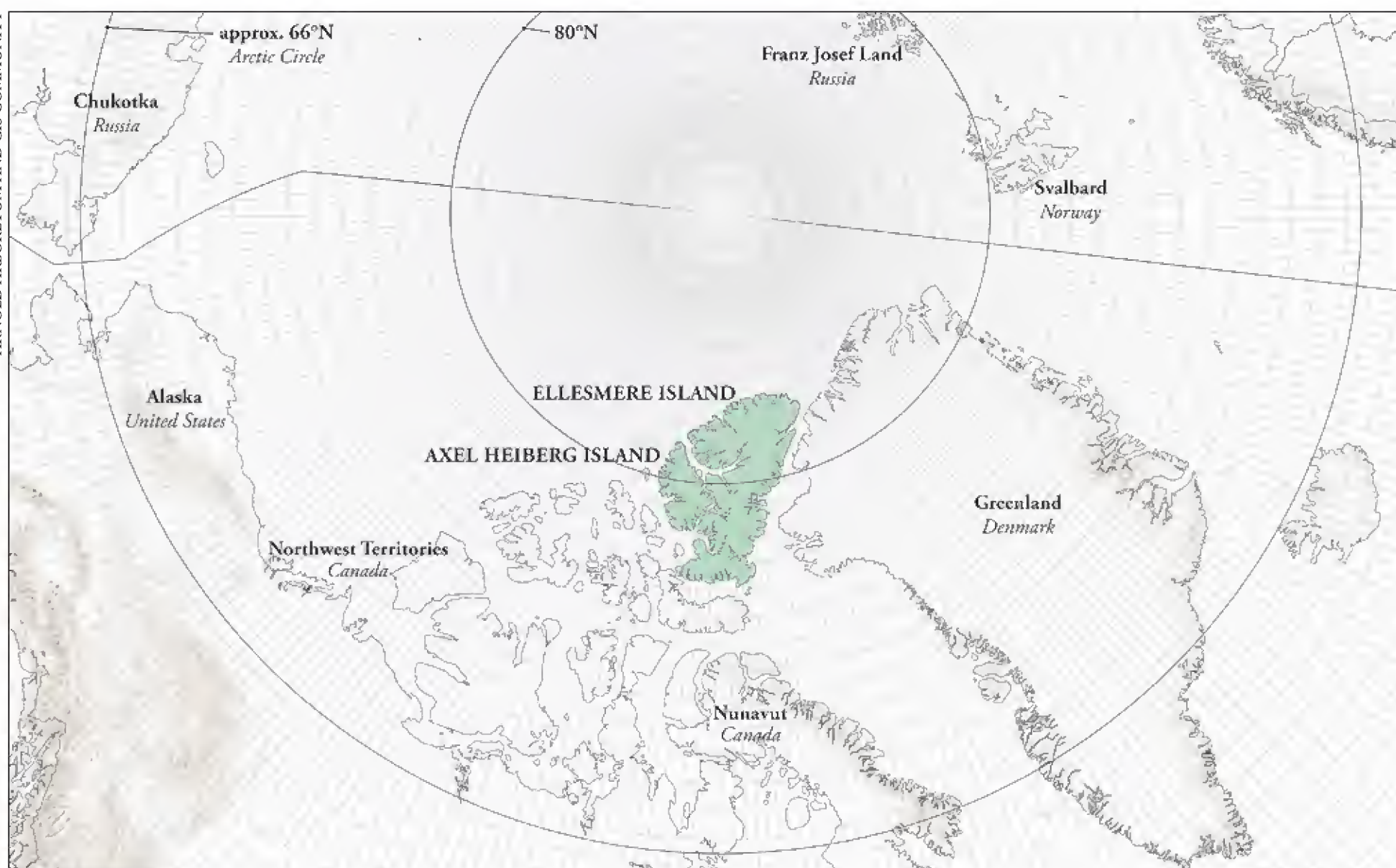


DANNY SCHISLER



MICHAEL DOSMANN

Metasequoia glyptostroboides is the only extant member of a genus that once flourished at warm Arctic latitudes during the early Cenozoic. Clockwise from top left: Seed cones hang on winter branches (notice that the deciduous leaves have already fallen), small pollen cones emerge in the spring, and trees at the Arnold Arboretum showcase an affinity for moist habitats.



The Canadian islands of Ellesmere and Axel Heiberg are among the most northerly landmasses on the planet, occurring well above the Arctic Circle. *Metasequoia* fossils have been recovered from both islands, at latitudes above 80°N.

Seedlings of *Metasequoia glyptostroboides* were grown along with those of two other deciduous conifers: bald cypress (*Taxodium distichum*) and tamarack (*Larix laricina*), whose fossil relatives were also common in warm Arctic floras during the early Cenozoic. These plants were grown for two consecutive years under the two different light regimes with otherwise identical conditions, including temperature, relative humidity, carbon dioxide level, and greenhouse irrigation. This research revealed that, in addition to deciduous leaves, which would drop during the prolonged darkness of Arctic winters, *Metasequoia* possesses physiological characteristics, such as high photosynthesis capacity and improved water-use efficiency, that help it take advantage of the weak but continuous Arctic summer light. This helps explain how this genus outcompeted other plants in the warm Arctic.

At the end of the two-year Jagels Experiment, we corresponded with the researchers and

obtained leaf tissue from *Metasequoia* seedlings grown in these greenhouse conditions. We wanted to learn how the ratios of carbon and hydrogen isotopes—slight variations of these elements built into plant tissues through photosynthesis—changed under different light treatments. These isotopes have been commonly used to understand ancient patterns for temperature, precipitation, and carbon dioxide level, and indeed, we discovered noticeable differences between seedlings grown under these alternate light regimes. Even more importantly, our work, published in 2009, established precise empirical relationships between isotope values of plant lipids and environmental water, allowing us to infer ancient moisture levels in this Arctic habitat.

New Technologies for Old Molecules

Experiments based on fresh *Metasequoia glyptostroboides* samples have enhanced the ability of researchers to interpret data from *M. occi-*

dentalis fossils, including biomolecules stored within the seasonal growth rings of the large trunks on Ellesmere and Axel Heiberg Islands. Hope Jahren—a geochemist at the University of Oslo, now well-known for her science memoir, *Lab Girl*—conducted analyses on seasonal variation of isotopes within these rings. Jahren and her colleague Leonel Sternberg observed high-resolution patterns in these isotopes, allowing them to reconstruct the impact of subtle climate variations on the growth habit of *Metasequoia* in the warm Arctic. They estimated a mean annual temperature for this high-latitude region to be around 55°F (13°C) during the Eocene—about double the present-day measurements. Relative humidity estimates were equally high: around 67 percent during the growing season and close to 100 percent towards the end of the growing season.

This climate information has direct implications for understanding global precipitation patterns during the early Cenozoic. At present, Arctic ice reflects back large amounts of solar radiation, keeping the global temperature low and simultaneously creating a steep temperature gradient across different latitudes. This equator-to-pole temperature difference significantly impacts the general circulation of heat—and moisture—through the atmosphere and ocean. Given what we know about Arctic temperatures, relative humidities, and carbon dioxide levels during the early Cenozoic, we know that this gradient of temperatures between latitudes would have been less pronounced, significantly impacting precipitation patterns. We used the relationship between environmental water and isotopes in fossilized *Metasequoia* leaves (established with the Jagels Experiment) to propose a model for early Cenozoic moisture patterns in the Arctic.

To our surprise, the relatively low hydrogen isotope values we measured were not compatible with the conventional understanding that the reduced temperature gradient from the equator to the Arctic should result in less precipitation during the long-distance transport of moisture within the atmosphere, depositing water with heavier hydrogen within the Arctic. Although there is no modern analogue for these high-latitude forests, dense forests at lower

latitudes, such as the temperate rainforests, offer clues that could explain these low isotope measurements. Due to moisture generated through extensive evapotranspiration of the vegetation, a portion of the heavy precipitation above these dense forests is composed of locally recycled moisture with lighter hydrogen. The greenhouse simulation in the Jagels Experiment supported this interpretation, demonstrating that photosynthesis under four-months of continuous light enhanced water evapotranspiration. These observations suggest that *Metasequoia* forests had a dynamic impact on moisture patterns in the ancient Arctic and may, in that sense, have even played an important role in maintaining the air circulation at the ice-free Arctic.

Climate Predictions

Strikingly, it took millions of years for the Arctic to transform from a humid *Metasequoia*-dominated forest into the landscape we recognize today, but the inverse warming trend now appears to be happening at a much faster rate. Over the last thirty years, Arctic warmth has accelerated along with rising carbon dioxide levels in the atmosphere. Arctic sea ice is melting, and glaciers are retreating at an unprecedented pace. In 2017, sea ice reached the lowest extent since the earliest time of satellite measurement in the 1960s. Recent global circulation modeling suggests that if the warming trend continues, by as early as the 2030s, the Arctic Ocean will change from perennially ice-covered to seasonally ice-free, further decreasing the temperature gradient between the equator and the poles. The weakened moisture delivery towards the poles will likely alter storm trajectories and increase temperature and precipitation anomalies, affecting the life of plants and animals, humans included, at the global scale.

In addition to informing what we know about ancient climate, *Metasequoia* has also contributed to future climate models. The scientific community has long accepted that atmospheric carbon dioxide has been one of the primary drivers for global temperature changes, but the rate at which temperature increases in response to changes of this greenhouse gas—a metric known



An artistic reconstruction of a *Metasequoia*-dominated forest and its surrounding environment at the end of the Arctic growing season during the middle Eocene (around 45 million years ago). The composition and density of the forest, as well as the hydrological conditions, were based upon fossil records and their stable isotope analyses.

as climate sensitivity—has been the subject of significant and ongoing research. Paleoclimatologists do not have the luxury of directly measuring ancient carbon dioxide levels; instead, they rely on indirect estimates, known as proxies, to make an inference. One of the most reliable proxies for reconstructing atmospheric carbon dioxide levels for geological eras that predate the oldest ice-core records is stomatal frequency. Stomata are small openings on the surface of leaves, and are the means through which terrestrial plants control the balance between absorbing carbon dioxide and losing water into the air. Species-specific relationships between stomatal frequency and atmospheric carbon dioxide (under high carbon dioxide levels, plants produce fewer stomata) thus allow scientists to predict one from the other.

The ideal plant to study this phenomenon should have a continuous, abundant, and widespread fossil record, along with living representatives to provide detailed comparative analyses and calculation. The genus *Metasequoia* fits the bill perfectly. The only challenge is that, as a deciduous conifer, *Metasequoia* has a very thin and fragile cuticle—the waxy layer covering its leaves—making it difficult to calculate stomatal frequency from fossils. Recent studies using improved experimental treatments and bioimaging techniques of *Metasequoia* fossils were successful, however, and surprisingly, work by Daniel Maxbauer and colleagues, based upon *Metasequoia* fossils from the Axel Heiberg Island and published in 2014, found that carbon dioxide levels during the middle Eocene (about thirty-seven to forty-seven million years

ago) may have been about half of what were previously estimated using other methods: a median of 424 parts per million (ppm) for the middle Eocene. If accurate, this work suggests that the *Metasequoia* forests in the Arctic were supported by much lower atmospheric carbon dioxide levels than previously thought.

This scenario does not portend good news for humans. The latest data from the National Oceanic and Atmospheric Administration show that carbon dioxide levels reached 405 ppm in 2017, exceeding concentrations throughout the past eight hundred thousand years that can be observed using ice cores. At the time when this article was written (in the summer of 2018), the level reached 410 ppm, marking the highest level since the late Pliocene, around three million years ago. From the pre-industrial carbon dioxide levels between 260 and 270 ppm to the current level, it took us less than two centuries to increase the atmospheric carbon dioxide level by more than 100 ppm. With this alarmingly accelerated rate, it wouldn't take long to reach levels that once sustained dense deciduous forests across an ice-free Arctic.

***Metasequoia's* Legacy Continues**

As we look toward future research involving *Metasequoia*, we can't help but marvel over the unintended consequences of scientific discoveries. When Japanese paleobotanist Shigeru Miki made the seemingly routine description of a new fossil species belonging to an extinct genus in 1941, he had no idea that its living equivalent was growing a few thousand miles away and waiting to be discovered. When Chinese botanist Zhan Wang encountered a splendid dawn redwood tree in Hubei Province (then part of Sichuan) for the first time, he could not have predicted that this rare conifer would produce important clues for understanding the vexing problem of climate change.

From the Chaney-Merrill Experiment to the Jagels Experiment, from the discovery of exceptional fossils in the Arctic to the applications of molecular isotope technology, science, as illustrated with *Metasequoia*, is a continuous endeavor in which new technologies facilitate new questions and, ultimately, new breakthroughs. Whether inconspicuously planted along a roadside in Sydney, Australia, or proudly



JONATHAN FONSECA

The authors examine *Metasequoia glyptostroboides* on the Bryant University campus. These trees were planted in 2006 during the Second International *Metasequoia* Conference held at Bryant and Yale.

showcased on our campus at Bryant University in Rhode Island, the dawn redwood has thrived through cultivation around the globe. In terms of sheer numbers, *Metasequoia* seems to have survived from the brink of extinction, yet its native population remains isolated with low levels of genetic diversity. While the natural population's long-term survival remains uncertain under the changing climate, what is certain is that, along with the advancement of technology, both living and fossil *Metasequoia* will continue to offer us invaluable information about its past secrets and the future of our global climate.

Acknowledgement

With limited pages here, we can only highlight the many exciting scientific inquiries about *Metasequoia* contributed over the past two decades. This is the duration since Hong Yang's first *Arnoldia* article on *Metasequoia* fossils and molecules, which was published in a 1998 special issue celebrating the genus. Readers can obtain further reading from the references and especially the proceedings of the three International *Metasequoia* Conferences. We would like to thank Jonathan Damery for discussing the structure and editing the manuscript, Chris Williams and Jonathan Fonseca for providing photograph images, and Yuyang Zhuge for illustrating the Eocene Arctic *Metasequoia* forest and its surrounding environment based on the scientific data we provided.

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The map in this article was created using Esri, USGS, NGA, NASA, CGIAR, N Robinson, NCEAS, NLS, OS, NMA, Geodatastyrelsen, Rijkswaterstaat, GSA, Geoland, FEMA, Intermap and the GIS user community.

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Overstory View

Jonathan Damery

Record tags at the Arnold Arboretum are as much a record of human lives as the plants. The oldest living accession—the sole remnant from 1872, the year the Arboretum was founded—comprises three shrubby winterberry hollies (*Ilex verticillata*, accession 147*A, C, and E), tucked near the North Woods. These were collected near Boston by Jackson Dawson, the Arboretum's first plant propagator, who was then overseeing greenhouses for the recently established Bussey Institute. If you indulge philosophical predilections, it is awe-inspiring to eye these wane suckering shrubs, which bore a smattering of red fruit this year, and realize that the shrubs have now persisted more than a century beyond the man who collected the original seed. As a rule, the Arboretum's oldest plants have all outlived their collectors, and at least some members of the subsequent plant generations, even material collected on our four expeditions this year, are destined to do the same.

Richard Powers explores this premise in his new novel, *The Overstory*. The narrative structure flexes time and space, at first introducing characters that exist in different decades (and centuries) and in different parts of the United States. All of the characters develop affinities for specific trees. In some cases, the relationship becomes a family legacy, as with the introductory characters: European immigrants named Jørgen and Vi Hoel move from Brooklyn to the Iowa prairie in the mid-nineteenth century. Jørgen plants an American chestnut (*Castanea dentata*) from seed he brought west. After Jørgen's death, his son buys a Kodak No. 2 Brownie—the classic model once used by hobbyist photographers—and, in 1903, he begins photographing the now prospering chestnut from the same location each month. A grandson continues the tradition, even as chestnut blight (*Cryphonectria parasitica*) sweeps through the eastern population, and the lens finally passes to a great-great-grandson named Nicholas. When Nicholas looks at the photos his family has produced, “three-quarters of a century dances by in a five-second flip.” Moreover, he sees a compression of human existence: “the holidays of his childhood, the entire clan gathering for turkey or carols, midsummer flags and fireworks.”

This generational project, in the nonfiction realm, is reminiscent of Chinese botanist Kaipu Yin's rephotography of trees and landscapes that Arboretum plant collector Ernest Henry Wilson documented in China in the early twentieth century. The resulting side-by-side comparisons were published in a collection, *Tracing One Hundred Years of Change: Illustrating the Environmental Changes in Western China*. The passage of a



A sixteen-foot slab of this giant sequoia (*Sequoiadendron giganteum*) was harvested from Kings River Grove, California, in 1891, as part of the Jesup Wood Collection, a project overseen by Charles Sprague Sargent. The slab can still be viewed at the American Museum of Natural History in New York City, where the annual growth rings reveal the tree began growing around 550 AD. Sargent, the founding director of the Arboretum, died in 1927.

century is evident in the landscapes and, more specifically, in the form of individual trees. Some have survived and, given their size at the time Wilson photographed them, likely survived at least the century before that. Others, however, have gnarled to a fist of limbs, broken and beaten. Still others are ghosts, replaced with glowing storefronts.

This effort to showcase non-human time is even more dramatic with Rachel Sussman's photography collection *The Oldest Living Things in the World*, because she only includes organisms (mostly plants) that are more than two thousand years old. Of course, one automatically thinks of bristlecone pines (*Pinus longaeva*), growing as bony skeletons in the White Mountains of California, where some specimens are more than five

thousand years old—a duration that pre-dates the invention of Sumerian script. But Sussman also directs attention to a colony of quaking aspen (*Populus tremuloides*) in south-central Utah, which has been spreading via underground roots for an estimated eighty thousand years. This marks the approximate time when humans began to successfully migrate from Africa—an astounding timeline, especially considering evolutionary anthropologists have shown that Neanderthals (*Homo neanderthalensis*) persisted in Eurasia for another forty thousand years beyond this.

Incidentally, Powers doesn't miss this ancient colony of aspen. One of his characters, Patricia Westerford, flees academic pariahdom (after publishing a controversial article about plant communication) and drives to the magisterial forests of the Pacific Northwest, but not before stopping to see the Utah aspen. "The thing is outlandish," Powers writes, "beyond her ability to wrap her head around." Likewise, Powers uses narrative to force readers beyond their personal footsteps—to literally view human existence from the overstory of time—which many environmental theorists suggest is essential for conceptualizing issues like climate change, with implications stretching far into the geologic future. Plants at the Arboretum—even lowly shrubs like Dawson's winterberries—provide a legible reminder of organismal time, a scale beyond ourselves, and as Powers demonstrates, narrative has potential to do the same.

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Hidden Gem Among Vines: *Actinidia arguta*

Rachel A. Brinkman

The hardy kiwi (*Actinidia arguta*) is a vigorous vine with fruits that you are unlikely to find at your local grocery store. The grape-sized nuggets are like the large kiwifruit (*A. deliciosa*), simply smaller and hairless. When you cut open the dusky fruit, which sometimes blushes from green to red, you'll see a firework design of lime-colored flesh with an inner ring of tiny chocolate-brown seeds. The taste of *A. arguta* fruit is similar to the commercial kiwifruit, but I find it milder, with less acidic tang. A connoisseur might describe a more sophisticated bouquet of flavors.

My first experience with this plant was back in college when a horticulture professor brought a basket of the fruit for the class to sample. I was amazed that the fruit existed—a bite-sized, thin-skinned version of one of my favorite fruits. I quickly became obsessed with the vine, but I did not encounter it again until I came to the Arnold Arboretum where I got to experience the plant as a whole: the glossy leaves borne on bright red petioles, the exfoliating bark, and the delicate and rather inconspicuous white flowers. Native to northeastern Asia, *Actinidia arguta* numbers among sixty different species in the genus, but only a handful of these can be grown in colder climates. The common species, *A. deliciosa*, is only hardy to USDA Zone 8, which means the species cannot be grown in New England, while *A. arguta* can survive to a remarkable Zone 3. The Arboretum currently holds five additional kiwi species, which all produce edible fruit in various colors and shapes.

Despite the taste and ornamental foliage, *Actinidia arguta* is a fast-growing vine that has escaped from cultivation in western Massachusetts, the New York metro, and northern New Jersey. This complicates any recommendation to introduce the species (which can climb more than thirty feet in a single season) as a more widespread fruit crop, although I have never observed any spontaneous seedlings on the grounds of the Arboretum.

Three of our accessions of this species represent wild provenances. A particularly note-

worthy plant (accession 905-85*A) is located on the second vine terrace in the Leventritt Garden, twinning up a steel trellis. This accession was received from the Chollipo Arboretum in 1985, which collected the seed on Mount Gaya, in North Gyeongsang Province, South Korea. I'm partial to its sweet wild-tasting fruit and its impressive girth at the base, which sprouts into twisting curls on the trellis. Two additional plants (accession 403-97*B and C) on the upper terrace of the Leventritt represent a wild provenance in Jilin Province, China, where seed was collected from a deciduous mountain forest by the North America-China Plant Exploration Consortium (NACPEC). These two plants have been trained to arch over the path, allowing visitors to view the beautiful structure of the vine from beneath.

Buds that produce flowers and fruits occur on the interior portion of the current year's growth—usually obscured beneath the foliage. *Actinidia arguta* vines are typically dioecious, which means that two vines are needed to produce fruit—one with female flowers, the other with male flowers. The flowers may look very similar, however, because most flowers have both male and female parts, but only the males produce viable pollen and only the females have properly developed structures for receiving pollen and developing fruit. To confuse matters, some plants can produce both male and female flowers, and others have been reported with perfect flowers. The species may even change sexual expression from year to year. The specimens of *A. arguta* that I have observed at the Arboretum have never been consistent in their fruit production.

Hardy kiwi may never become a common fruit crop, and perhaps, given its swift growth and ability to escape from cultivation, it never should. Yet as you stroll through the pathways of the Arboretum, don't forget to stop to investigate our winding vines; you may discover hidden gems nestled beneath the leaves.

Rachel A. Brinkman is the assistant manager of horticulture at the Arnold Arboretum.





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